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BY
H. GODWIN

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POPULATION INTERSPERSION: AN ESSAY ON
ANIMAL COMMUNITY PATTERNS*

BY CHARLES ELTON

*Bureau of Animal Population, Department of Zoological Field Studies, Oxford**(With one Figure in the Text)*

Most of the great advances in ecology during the last quarter century have taken place either within the field peculiar to plant ecology, or in the demology or population problems of animals. On the one hand we have seen much progress in the general classification and nature of plant communities, their succession relations, the physiological reactions and symbionts of particular plants, soil organization, ecological genetics, and Holocene vegetation history. On the other hand, there has been an outburst of field research on the density of animal numbers, and on the age and sex structure, movements and fluctuations of animal populations, accompanied by some rather exciting experiments in the laboratory on self-limitation, competition, parasite-host and predator-prey relationships, backed by ambitious mathematical theories of various kinds.

These main fields of research have brought into clear relief some of the intrinsic differences between plant and animal ecology, and especially the manifold consequences of animals' power of movement. But between these two fields lies a tremendous region in which plant and animal ecology join, and where all the discoveries made in either should logically be synthesized to give us at least a working model of how whole ecosystems are arranged in nature, and how they work and interact. In this region lie studies of animal community structure and pattern and energetics, the description of animal habitats, relationships between plants and animals in respect to food, cover, pollination, dispersal of fruits and seeds, and other reactions of animals on vegetation and plants on animals. It includes a huge range of facts about animal behaviour and distribution and many problems involving the general equilibrium in nature. For it must be remembered that such a general equilibrium does exist, even though it is subject to recurring fluctuations of all sorts, and even to complete local breakdowns of the ecosystem such as the poisoning of the faunas by outbreaks of blue-green algae (Prescott, 1939), and the desolation of vegetation by field mice, locusts or caterpillars. I shall attempt to explore a few general laws regulating the distribution and balance of communities that do not seem to me to have been looked at as a whole. I am quite aware of the depth of our ignorance of many matters that take part in the completion of such a picture. It would be absurd at the present time to hope for completeness. Nevertheless, I am absolutely convinced that we are on the threshold of a period when synthesis of animal and plant community facts and concepts will not only be possible but necessary, if we are to interpret ecological phenomena fully, and see them in the proper contexts. I think that the ocean of ecological facts has reached a dangerous tide level, and the ideas I wish to develop here may have a certain value as a raft to float on. The general ecologist needs a raft from which to cast his sampling plankton net. The plankton may be patchy and the work of collection and synthesis very laborious,

* The substance of this paper was read as Presidential Address to the British Ecological Society on 7 January 1949.

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but if he has some clear principles by which to sort out the material, great advances are possible. But one should bear in mind the excellent remark of Thoreau that 'The volatile truth of our words should continually betray the inadequacy of the residual statement'. In case this paper comes to the attention of naturalists as well as ecologists, I would like to add that the ideas in it were largely obtained while pottering about in the woods and elsewhere in the country, and during the necessary period of rumination entailed by setting and labelling specimens and processing the records of some thousands of 'ecological incidents'.

I have sat through a great many papers at meetings of the British Ecological Society during the last 25 years, and the dominant impression retained is of the extreme range and fragmentation of ecological knowledge. At times one's mind has almost seemed to crack in the effort to understand the relevance to the main purpose of the Society of some specialized piece of discovery about plant or animal life. Synthesis is still rather limited, owing to this enormous area and variety of research. There is, of course, no doubt that the quality of research can only be kept high by some specialization, by focusing deeply on limited fields. But what is the ultimate goal and purpose of all this ecological research? Why do we continue to meet at all and listen to each other's fragments of discovery? Not, I feel sure, just to understand about root fungi or the zones of salt-marsh vegetation or the bee visitors to fruit trees or the changes in numbers of arctic foxes or gall-flies, however fascinating these are in themselves.

I have roughly analysed the first 16 years of the *Journal of Animal Ecology*, i.e. 1932-47. Of 312 papers, only 40, or 13%, were concerned with ecological surveys of whole animal communities. By this I mean surveys attempting to describe a large sample of the different taxonomic groups present in habitats, not those dealing say only with birds or amphipods. But only 8% of the whole were concerned with British communities. These twenty-five surveys included six terrestrial, nine fresh-water and six marine habitats or complexes; two were general, and two marine Holocene. Of these the terrestrial ones were the least complete. There were only four papers that discussed community composition in general, i.e. about 1.3%, and two of these were in flat contradiction to one another.

During the same 16 years the *Journal of Ecology* published 268 papers, rather fewer than the other *Journal*, though some made up for this by their majestic size, and 253 dealt with plant ecology primarily. Of these no fewer than 68% were studies of plant communities, 35% referring to this country, 25% to other countries (mostly Tropical). And twenty-one (or 8% of the total plant papers) dealt, often in a highly philosophical way, with theories and methods of community analysis, and there was some measure of common agreement resulting from them. (I omit five animal community surveys. If they are added to those in the *Journal of Animal Ecology*, they only slightly increase the percentage of community papers.)

So it would seem that plant ecologists have made considerable headway in the organization of their part of the whole subject, and that a great deal of their information is already in a partly integrated form. They have not solved many problems finally, but they do begin to know what shape the problems are. Animal ecologists, on the other hand, have been concerned so far with fragments, sometimes quite large ones, but nevertheless fragments, and the split between the plant and animal ecologists' outlook is quite considerable, and is reinforced by a great degree of separate training in universities. It must be pointed out here that none of these surveys analysed above was or claimed to be describing completely

all the forms of plant or animal life even on a sample area of a habitat, or to represent more than one local variant of a complex system or formation. Animal ecologists have usually had to leave out the parasites, which are a legion, and many free-living microscopic animals; plant ecologists also omit most of the parasites such as fungi, bacteria and viruses. They omit even the very numerous macroscopic fungi, and not infrequently the cryptogams, or at any rate the lichens, and the microscopic algae. The plant ecologist also usually leaves out the animals, and the animal ecologist usually makes an exceedingly sketchy record of the plant background.

In making these preliminary remarks, I do not wish to seem critical. There are perfectly good reasons why this situation exists in ecology. There are more species of animals than of plants, even if we include the fungi and other lower forms. Animals usually have complex life histories, of which the earlier stages may be ecologically the most important though harder to find and to identify. Animals have activity rhythms, and are often inconspicuous or invisible while resting, either by taking refuge under cover or by camouflage. Their seasonal occurrence in an easily identifiable or observable form may be brief and complicated by weather affecting activity. All animals move about to some extent; amongst other things, this makes many of them hard to catch, or hard to follow and observe. Furthermore, animals live in a number of habitats, like carrion or caves or lake bottoms or the abysses of the sea, from which green plants are absent, i.e. animals inhabit a more complex range of habitats.

Take one simple example of the problems the ecological surveyor of animals may encounter. In Wytham Woods, on the afternoon of 14 August 1948, I visited a wide grassy and rushy ride through oak-ash-sycamore woodland, which had a magnificent population of tall teasels in flower. The plant ecologist could note down '*Dipsacus fullonum* ab.fl.' On these flowers were scores of fresh peacock butterflies (*Vanessa io*), also seen sunning themselves on the bracken of the woodland edge. With them were a dozen commas (*Polygonia c-album*), several fresh brimstones (*Gonepteryx rhamni*), and a few elderly silver-washed fritillaries (*Argynnis paphia*), also one or two gatekeepers (*Maniola tithonus*), green-veined and large cabbage whites (*Pieris napi* and *brassicae*), a brown argus (*Aricia agestis*) and some bumble bees. The day was dead calm, warm and sunny. Next day at the same hour, *Dipsacus fullonum* was still ab. and fl., but there were no butterflies on them except a few peacocks, and these were hanging on with difficulty against a strong west wind, though the weather was still sunny. Only by repeated and frequent visits would even an apparent relative abundance of butterflies be established, and this would need to be interpreted very cautiously, because absence could be due to four things: inactivity, death, emigration, or inefficient observation (as on a small number moving over a large area of habitat).

Then, if we want to know where the peacock butterfly had bred, we are at a loss unless we know its food plant (in this case nettles), whether its caterpillars bred on nettles within the woodland canopy or at the edges of surrounding fields—or still farther away. The large white might even have spent its early life in some Baltic farmer's cabbage patch.

Annual fluctuations in numbers add another problem; in 1947 hornets (*Vespa crabro*) were commonly seen cruising about this teasel patch. In 1948 there was none. This could be due either to the accidental proximity of a hornet's nest in the first year, or to a general scarcity of hornets in the second year (which was indeed observed), or to both. From this we see that a survey of animal communities is a long and tricky task.

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The ultimate goal of an ecological survey I would suggest is: 'An attempt to discover the main dynamic relations between populations living on an area.' This area has usually been taken as one of the major ecosystems such as a lake or a river or a wood or a salt-marsh or a sand-dune complex, i.e. a system that is strongly interlocked in its parts but shows some fairly well-marked boundary with neighbouring ones. I want to suggest that the unit we should choose for detailed study could be much smaller than this, and yet should be known in such a way that it can be related to the system as a whole.

This introduces the main subject of this paper: habitat patterns as they affect animals. We have had previously two distinguished presidential papers bearing on this subject, one in 1941 by Captain C. Diver, who dealt with micro-topography and habitat loci, as he had studied them in his great Studland Heath survey,* the other by Dr A. S. Watt (1947), on 'Pattern and process in the plant community'. These earlier contributions encourage me in the belief that there is here an important and somewhat undeveloped aspect of ecology in which different specialists may find great common interest, and which may give both them and the naturalist some help in overcoming the obstacles of building up survey of ecosystems.

Ecologists are going to have to do a great deal of hard thinking if they are to achieve even one of the scientific recommendations mentioned in the White Paper on conservation (Ministry of Town and Country Planning, 1947, p. 70): 'The biological survey of National Reserves and the conduct of wider surveys with the ultimate aim of carrying out a thorough survey of wild plant and animal life throughout the country as a continuing process.'

Imagine, for a moment, a potential habitat in which no organic life has yet appeared at all: a bare dune, mudflat, hill slope, river bed. When we set out to describe any spot on such a potential habitat, the first thing we do is to determine its position in space and time. We give it geographical location, usually a place name, from which by implication we can derive its position on a grid of geographical co-ordinates (now added to the modern 1 in. map), its height above the sea, nearness to salt or fresh water, and to a limited extent consequentially the aspect and main gradient.

These and the date have for a long time been the only things that the taxonomist put on his labels, though that is changing greatly under the impact of ecology. When we come to the detail of minor topography, we find it difficult or impossible to describe it quantitatively, because it is mostly arranged in quite irregular patterns of hollows, hillocks, ravines, etc. It is exceptional to find any fundamentally periodic arrangements of such minor topography, such as occur in Arctic soil polygons, or between cracks from drought. The habitat is in a state of 'undiluted geography' formed from local differences in shape of ground, water table, water quality, aspect, soil texture, and rates of erosion and deposition and comminution. It has been necessary to mention these rather obvious primary features, in order to contrast them with the next stage when definite periodic patterns in space begin to appear.

Let us next imagine vegetation colonizing and modifying this surface, through succession phases perhaps up to something like a stable climax, or perhaps lodging at some transitional stage. As soon as you have populations of plants mixed together, an orderly pattern begins to be laid down. The interspersions of one population with that of another species necessarily means that the individuals of the first are partly separated from neighbours of their own

* This paper has not so far been published, but some cognate ideas about the plant carpet as a mosaic of animal habitats are discussed by Diver (1938). These have a close bearing on topics discussed in the present paper.

species by those of other species. And this leads in turn to several types of periodic arrangement in space, of more or less regularity: in other words, to a habitat pattern, with many small components repeated at spaced intervals. It is these small components that form the primary habitat units for animal communities. First, the dominant plants, especially where they are trees or shrubs, tend to have equal spacing, such as we may see in a developed elder scrub or beechwood. That is brought about, as we know, by root and canopy competition. Secondly, the original minor differences in the ground, which were irregular, may in time and with the development of vegetation and other processes gradually tend to be smoothed over. This happens with humus formation in a wood, and we might expect to find increasing regularity of the spacing between say dominant trees, resulting from the modification of the primary habitat by plant activity. Where this does not happen completely, we would find the original irregularities of the primary topography and soil still appearing, though greatly modified by the vegetation, e.g. in such things as deep hollow, ravine, water catchment, and so on. Although these do not provide a regular periodic spacing of minor habitats, they add variety to the habitat. Thirdly, there are various minor successions set up, mostly through the dying of individuals. The most imposing of these is the falling of old trees and the formation of glades which become filled up anew by saplings. Jones (1945) has pointed out how such gaps fill up and tend to maintain a general canopy even though the trees are not all of the same maturity. The openings that occur through such minor successions will normally be distributed somewhat at random, though they must in turn be based upon the basic vegetation pattern that gives rise to them.

Another point about the general vegetation pattern needs mentioning. The dominant plants, say a beech tree, or a grass tussock, will tend to have the greatest regularity of pattern, and at the same time the greatest contact between their canopy. But they will always create around them a periodic centre represented by the tree trunk or tussock, and a concentration of leaf and leaf fall. Those species that are less abundant, i.e. the majority, will be dispersed in either of two ways. If they are directly dependent upon the dominant, as with moss on a tree trunk, or a saprophytic orchid on beech humus, they will or will tend to follow the regular distribution of their dominant. Conversely, those that can only live outside the influence of the dominant, like bracken in a wood, will tend towards some inverse periodic distribution in the interspaces. The second type of distribution is of the less abundant plants that are not geared on to the primary vegetation pattern, but occur in a random manner throughout the community. Not only will these be less regularly or quite irregularly spaced, but the distances between each plant or patch or society will tend to be greater than between the dominants.

I get the impression that although plant ecologists are quite aware at any rate in some level of their minds, of the patterns I have been talking about, they have nevertheless rather taken them in their stride, and have devoted comparatively little quantitative research to the subject, other than the excellent kind of micro-succession studies illustrated by Watt's Breckland work. There are few data, except for certain types of trees dealt with in silviculture, for the minimum or mean distances between plant units, i.e. components of patterns in a community, the frequency of glades of a given size in a forest area, the random or non-random distribution of different species in space, or the areal size of each component like a tree with its canopy. Nor do we have a picture of the leaf litter or soil patterns associated with such vegetation.

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So far we have arrived at an idea of the habitat being a mosaic of centres of different kinds, really centres of action in which interspersions between populations tends to be complete and ecological dynamic relations (at any rate among invertebrates) at their strongest. These centres I shall call *minor habitats*: single trees, homogeneous clumps of saplings, societies of herbs, grass tussocks, units of aquatic plants on a particular patch of river silt, patches of reed swamp along a river. Although they may be so close and homogeneous (as with a *Phragmites* swamp or a crop plant) as to lose the qualities of obvious patterning, usually they are spaced out and repeated more or less in the same form, partly regularly and partly irregularly. There are two main kinds of pattern. I will call them *area* patterns and *boundary* patterns. The first is what you see in an air photo of a wood or scrub or in the pools on a salt-marsh or on hillocks in a dune system. The second is seen along the seashore or the margin of a pond, lake or river, in field and road boundaries of hedge or wall or grass verge, and in small streams. In the vertical dimension, a tree trunk presents a boundary pattern. In the boundary type, there is broadly speaking the width of one minor habitat, and this is strung out in two instead of three dimensions. For example, compare the occurrence of buckthorn or elder in a chalk hawthorn hedge with their distribution in a reverting field or a wood.

Let us now consider the interspersions and patterning of animal populations. They partly follow the arrangements of the terrain and the vegetation, but they also impose new patterns of their own making; these may be quite independent of the others, and of each other, but are often periodic in space. Take first the groupings around *minor physiographical habitats*. In this category we may place the faunas of woodland or other springs, which are restricted to the head-springs of a stream. These springs are determined by the geological strata, and there is no regularity in their spacing. Nevertheless, they form small loci separated by some distance from the next. In a similar category are the patches of fine mud, coarse silt, and gravel that occur in a river, according to the contours and speed of the currents. Mud-living forms of mayflies, chironomid flies and Mollusca often have a patchy distribution according to the distribution of the substratum. But such arrangements are so irregular and their texture and scale vary so greatly that we are hardly justified in calling them regular patterns at all. It is when we come to vegetation that the influence of regularity is felt, as in the grouping round *minor habitats formed by plant individuals or societies*, e.g. an oak tree, a patch of sycamore saplings, or a *Juncus* tussock. Here it should be noted that I shall use the phrase 'minor habitat' in a relative sense, not to describe absolute size. *Microhabitat* I shall reserve for the detailed parts of a minor habitat, as 'twig', 'under-side of leaf', 'flowers', 'under bark', 'bones', etc.

Each plant species usually has a nucleus community of herbivorous animals, almost entirely insects, confined to it for food, or at any rate very characteristic of it. They do not always necessarily dwell on the plant or near it; indeed, life histories completely on one plant are not the commonest thing to find. Most herbivorous insects spend a substantial part of their life associated with the plant, but the other part in the soil, moving about, lodged in some refuge, or even on another plant. These monophagous and characteristic herbivores are being indexed by Dr O. W. Richards, and gradually published through the Society's *Biological Flora*. This requires enormous labour and discrimination, and will give a most valuable basis for studying the minor communities on plants.

In the selection of plant faunas already issued, the number of specific and characteristic herbivores for the British Isles varies from none in *Cladium mariscus* and *Allium*

vineale to thirty-eight in the common maple (not counting flower visitors, which can in some cases also be specific, or at any rate highly characteristic). In between we find numbers like four on *Tamus communis* and *Atropa bella-donna*, ten on *Glyceria maxima*, twenty on *Rhamnus cathartica*, while the genus *Polygonum* has twenty-nine and the genus *Juncus* thirty-three. These figures cannot have a precise meaning in detail; but they do indicate the sort of scale we may expect to find, although on some large, ancient and complex trees like the oak, the numbers will be very much larger.

Such herbivorous animals belong almost entirely to the insects, and to the five largest orders: bugs, butterflies and moths, beetles, flies, and the Hymenoptera (and of these substantially the sawflies and gall-wasps). Flower visitors could be added to these other herbivores, and will be referred to later on. For instance, although the black nightshade (*Tamus*) has a very small number of insects feeding on its leaves or stems, it possesses flowers that are extremely attractive to flies and some other insects.

Besides these restricted forms, there is a large number of more polyphagous herbivores that may be equally or more important and abundant, and when we come to carnivores, this is still more the case. Nevertheless, the periodic spacing of the minor plant habitats or components of the pattern must bring about a periodic distribution of density of all these forms, whether they are specific to the plants or not. This can be illustrated by a diagram, for any given herbivore. First take the imaginary instance of population density of a specific birch-tree aphid, the trees being scattered about in a developing oakwood. The vertical co-ordinate is population density, the horizontal one lateral distance (Fig. 1*a*). The flat-topped peak represents a group of birches, the others individuals.

If we were plotting the density of a parasite which attacks only this host, there would be a similar grouping (Fig. 1*b*), that is, if the parasite succeeds in finding all the minor centres. If, however, we are plotting the distribution and density of a carnivore such as a lacewing, whose larva and adult are attacking various arboreal aphids, its distribution, though still in patches, would be contoured in some such way as in Fig. 1*c*. The important point at the moment is the discontinuity or contouring of the population distribution. As far as I know, real examples of such distributions have not been measured; nevertheless, the situation must tend towards something like what I have drawn.

When one works for some time in a deciduous wood, it begins to dawn on one that these minor habitat centres have very characteristic community compositions. Thus one soon learns to expect caterpillar abundance on oak, aphid abundance on sycamore, leafhoppers on ash, chrysomelid beetle abundance on *Mercurialis*, and butterfly-caterpillar colonies on nettles. I mean that not only is the species composition of the herbivores different, but also the dominance of different types of herbivore, or as one may say, there is a spatial separation of the chief key industries.

There are, however, some forms that do range very widely; for example, the tree long-horned grasshopper (*Meconema thalassinum*) is found on oak and ash and sycamore. Carnivorous insects are not usually very restricted; some, like the common green lacewing (*Chrysopa carnea*), are widespread on trees and shrubs that carry aphids; but the snake-flies (*Raphidia*), though not infrequent on oak, where they find excellent crevices to lay their eggs, are seldom found on young sycamores which have very smooth trunks and twigs. Furthermore, I have formed a strong impression that except for certain animals like spiders that broadcast their young, and are often fairly wide in their feeding tastes, these minor plant centres tend to keep their integrity, and that such random searching by

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animals as occurs results either in finding the right habitat or in death. In other words, the complications introduced into ecological survey by purely accidental visitors are not very serious so far as herbivorous forms are concerned. Many of the accidental visitors come from other minor communities that I shall mention. This conclusion is a natural one, since arthropod herbivores are, after all, adapted in their responses to finding the plant they breed on.

Now we come to further *population patterns superimposed by the activities of animals* that range beyond a single minor vegetation unit. This usually arises from the way that birds

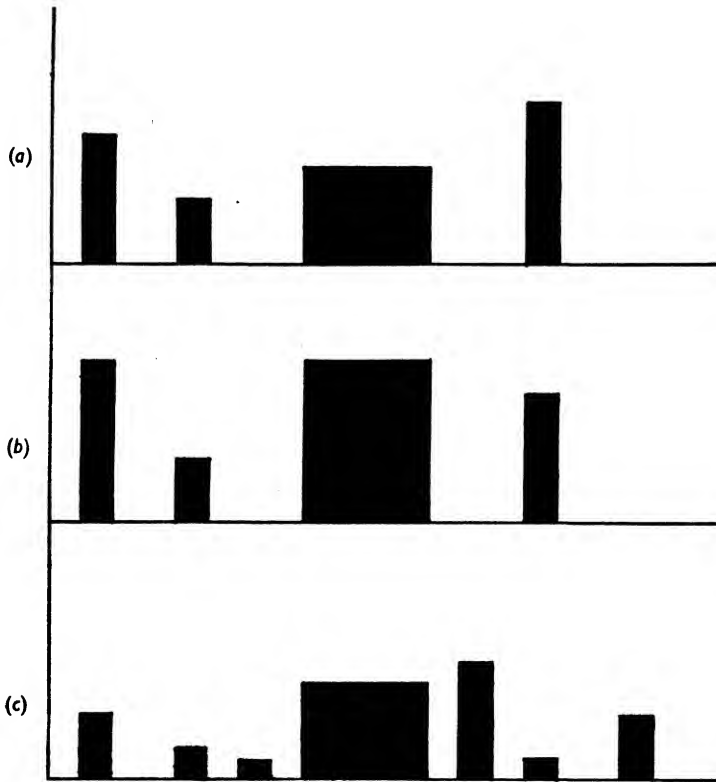


Fig. 1. Theoretical diagram representing a transect through some major habitat such as a wood, at a time when the animals concerned are confined to their minor habitat centres, and not undertaking lateral migration. The vertical ordinate is population density, the horizontal ordinate is lateral distance. (a) A monophagous herbivorous insect, (b) a monophagous hymenopterous parasite attached to it, (c) a polyphagous predator.

and mammals, and some social insects, establish refuge centres from which they move over a foraging area, which are not infrequently territorial, i.e. the boundaries are not merely determined by the distance from home, but by active competition between neighbours. Such territorial spacing is well known among many birds during the breeding season (e.g. willow-wren, kingfisher, tawny owl, oyster-catcher), and it frequently occurs among rodents such as mice and voles, and in some predators like the badger. Ants sometimes produce similar periodic arrangements, and in the wood-ant (*Formica rufa*) they are certainly in part territorial. In dense conifer woodland the nests may be spaced out in a boundary pattern or chain of beads; in more open woodland they may form an area

pattern, a sort of Balkans among ants. The yellow ant (*Lasius flavus*) that forms mounds in pastures is really an aphid farmer, keeping its flocks on the roots of grass, and these mounds impart a clearly periodic pattern to some fields.

Let us note two general dynamic consequences of the patterns so far mentioned. In all of them, the population of each species of animal tends to a periodic contouring, not to a general distribution of density at random. This means that theories about population changes and interaction, which are nearly all based upon conceptions of mean density, must learn to take account of the fact that populations are split up into groups or centres of action. A. J. Nicholson has explored this point a little, but it needs far wider recognition, and its full consequences still have hardly been touched by mathematicians. The unit to which we can attach the idea of complete dynamic population interspersion is frequently this small minor centre of pattern component, i.e. an oak, a group of aspens, a patch of water *Ranunculus*, a small spring, or a glade in a wood with a population of red campion in turn forming patches within it.

The second consequence is the lateral movements from and between centres, discussed later on.

The distribution of density will usually vary between day and night, where these larger ranging species are concerned, so that during the daytime we might find wood-ant density and activity distributed in decreasing amount with a high concentration near to and in the nests, and at night entirely confined to the nest centres. A tawny owl population would have the reverse alternation. The population pattern therefore has diurnal cycles in contouring, on which will be superimposed seasonal degrees of territorial or social activity, as well as year to year fluctuations in total density.

Man has imposed some of the most regular periodic patterns of all upon soil and vegetation, by his system of crop cultivation, which incidentally tends to produce a more complete canopy of unispecific dominant vegetation than much natural vegetation, at any rate at maturity. In simplifying, or as some would think over-simplifying, his crop stands, man has nevertheless been compelled to adopt a rotation system that is a crude substitute for the simultaneous processes of soil renewal that went on in the original vegetation. This has brought about a very marked major habitat interspersion, e.g. of cereal, grass or clover or roots, and fallow.

At this point, I would like to put in a suggestion, for it is nothing more, that the charm that we feel about natural ecosystems, which forms part of the driving force behind conservation, is based partly upon the mixture of order and disorder that I have been trying to analyse. It is probably a deeply instinctive satisfaction, and it undoubtedly comes out also in the field of art, both in music and poetry, and even in architecture. How often one has been grateful to find an irregular garden associated with the formal lines of a building, or a tree whose seed was blown or perhaps brought accidentally by a bird, breaking the regular alinement of a street.

Let us now continue with the survey of minor habitats, for by doing so we shall find it possible to split up our faunal lists into more easily handled units for field study, and at the same time build up a general picture of how major habitats are patterned and their populations distributed. These habitats can be taken in a fairly logical order.

There are first of all a number of *detached parts of living plants*: resting stages like nuts and seeds, and pollen. In nature the former do not usually form aggregations sufficiently large to merit the term of minor habitats in the sense I have been using it—they would be

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better described as microhabitats. These frequently contain stages of herbivorous invertebrates. But man by his mechanical skill in assembling large quantities of seeds, nuts, roots and other living parts of plants, has created not only minor habitats like corn-ricks and potato clamps, but much larger ones in the form of grain stores and so forth, with all the consequent problems of stored product insect pests. These need not be analysed here, except to draw attention to the curious fact that the great bulk of the fauna of stored products consists of small beetles, moths and mites, and that the communities are, apart from a few parasites, composed of herbivores or scavengers that often also practise cannibalism on their own and other species. We have, in fact, the extraordinary phenomenon of an almost one-consumer-layer community combining within itself the herbivore and carnivore role, and also practising self-limitation. And as far as I know it is the only type of community that has ever succeeded in heating itself out of existence by ordinary metabolic activity, as occurs sometimes among grain weevils (*Calandrá*).

Such aggregation by man, of what are normally small units, also occurs in sewage farms, timber yards, meat and skin stores.

Another aspect of these small detached living parts of plants is dispersal. The interspersions and movement of animals among plants has made possible the development of special seed and fruit dispersal and of pollination mechanisms, the animal acting as a minor habitat, or more frequently quite a microhabitat, and the detached part of the plant becoming a temporary parasite upon the animal. With seeds it may be ectoparasite (as with the enchanter's nightshade on man's clothes), or endoparasite (as with guelder rose fruits inside a blackbird); pollen is, as far as I know, always an ectoparasite. These reproductive products are here termed temporary parasites because they do depend upon the energy of animals moving about, and although the amount exploited may be often quite unmeasurable, the principle remains. When an insect carries honey away as well as pollen, it may be said that the parasitic activity is paid for, and this would undoubtedly be an interesting budget to work out! These consequences of the interspersions of animal and plant populations are mentioned here because they are essential for the continued existence of the community; because they bring the dispersal of female and male reproductive products of plants into a correct alignment with fungal and animal parasites that live on animals as minor or microhabitats; and because pollination by insects has made possible the development of some of the more important social insects, which themselves form further minor habitats for other animals.

The *bodies of living animals* are themselves the habitats of special communities of parasites, which have been surveyed to a limited extent, and which form part of the field of epidemiology. The principles of population interspersions are deeply involved in this field, but here it will only be mentioned as a vital secondary consequence of the community pattern shown by the host species.

Animal artefacts form important minor habitats. These are of a great many different kinds. First of all various burrows in the ground made by mammals like rabbits, foxes, badgers, moles and mice. In the nests of these mammals there is a considerable special fauna, some of it (especially with moles) confined to that species and not breeding elsewhere. Other mammal nests on or nearer the surface, as those of hedgehogs, bank voles and of ground nesting birds also, contain special assemblages of insects, including beetles, flies, parasitic Hymenoptera, Collembola, ticks, mites and fleas. Some are bloodsuckers, and therefore depend directly on the host, others are saprophagous, others carnivorous on the

previous species. The conditions are quite peculiar, especially in being highly sheltered and kept warm.

Nests of squirrels in trees, of bats in tree holes and buildings and rock holes and of various birds in trees and tree holes provide further special habitats. A tawny owl's nest is quite a startling special environment to collect in, owing to the extremely strong smell of ammonia that it gives off. We have not yet got a complete picture of the faunas of bird and mammal nests, though a great deal of scattered work has been done, and several important studies still remain to be published. They are enough to indicate that there is a strong difference between ground and arboreal nests, and between those of some of the species, and that they contain a considerable number of arthropods, either not found in other habitats, or else shared with decaying plant or animal matter.

Ant, bee and wasp nests have received a great deal of attention from entomologists. Well over a hundred kinds of insects have been found exclusively dependent upon the nests of British ants; and Donisthorpe's book on them (1927) should be consulted, for it is fascinating and also shows how much more work there is for naturalists to do in this field. During a rather complete ecological study of nests of the thatching ant (a close subspecies of our wood-ant, *Formica rufa*) in North Dakota, Weber (1935) found about thirty species of animals in one nest. Donisthorpe (1930) found twenty-four true myrmecophiles on this species' nests in Windsor Forest, the same number with *Lasius fuliginosus* and thirty-six with *L. brunneus*.

Wasp and hornet and bumble bee nests also contain a number of parasites and guests and carnivores.

If we were to list all the much smaller artefacts of animals, such as nests, burrows, food stores, etc., we should find a great number of other species dependent upon their activities, and therefore grouped around them in minor or microcommunities. This leads on to another large sector of the subject: secretions and excretions.

Of *plant secretions* the most important are honey and honeydew. The distribution of these on different plants plays a clearly defined part in the patterning of any community. Although there has been a great deal of general observation and some experiment upon pollination, the listing of species attached to particular plants is very incomplete except for the hive bee, and here the results are mostly averages of day's work, and we have not a very exact picture of how different insects move about and visit the minor plant units. Here is an attractive and productive field for exact ecological work. It is particularly necessary in such study to separate the casual visitor from the frequent and important pollinator or even the important robber, and to dovetail the data into a seasonal history of visiting species.

Honeydew secreted either by leaves themselves or by aphids sucking the leaves determines the local aggregation of visiting insects to certain trees, e.g. the sycamore or the lime. One would like to know much more clearly what honeydew actually is, or in what senses the term is used, and whether it is the same stuff on different plants, and how the collecting insects react to its presence on various plants. But such secretions and also sometimes sap flows (as from the elm) form an additional unit in the total habitat pattern.

The *secretions of animals* are especially important in the manufacture of the wax combs of bees' nests and the papery structure of wasps' nests; and they play a big part in some of the food chains we find both there and elsewhere, e.g. secretions from guest insects that enable them to become tolerated in ants' nests, and the direct collection of honeydew by

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ants from aphids. But animal secretions do not seem otherwise to be important in this country as a source of minor habitats.

With *excretion* the situation is different. Mammals and birds produce large quantities of dung daily, especially the larger herbivores. American workers (Mohr, 1943) state that beef cattle produce about half a hundredweight of dung daily per 1000 lb. of animal live weight. That is to say that a cow weighing 1500 lb. might easily produce over 12 tons of dung a year, or say 6 tons on an acre. It is not surprising that dung is therefore an important minor habitat for animals, and essentially one that occurs scattered over the foraging area of the animals that produce it. Mohr has made a really intensive study of this community in Illinois, many of the genera of insects being the same as ours, and no doubt the principles he worked out would apply here. There were altogether about eighty species concerned, mostly flies and beetles. As a community it operates only in the warmer times of the year, and as here there is quiescence in winter. Mohr observed several seral stages, and there were parasites and predators. For instance, the staphylinid or rove beetles entered as soon as the pioneer flies and beetles had made galleries in the gradually drying dung. Later on other beetles arrived, some of them carrying mites on their bodies. The species taking part also differed according to the season, a thing we shall note for carrion also. The fauna also differed somewhat if the dung was dropped in the shade instead of the open. In various types of mammal dung, including manure heaps, in the Windsor Forest area (see p. 14) Donisthorpe (1939) found 100 species of beetles.

Hammer's study (1941) of the flies in cattle dung in Denmark, though confined to that group and admittedly not including all the families of flies with equal completeness, nevertheless shows the importance of this animal community, and the great complexity even within such a minor habitat. Sixty-four species of flies were studied, and most of these had coprophagous larvae, the rest being carnivorous. The former were mostly confined to dung, the latter sometimes occurring more widely, as in carrion also. The habits of the adults varied greatly, some being liquid dung-suckers, some blood-suckers, others predatory on insects, or flower visitors. The seasonal life histories also varied a great deal. Similar coprophagous communities are known, but have not been completely studied, wherever smaller mammals or birds have concentrations of dung, and part of the nest fauna is formed by such species.

We now come to *decaying plants* and animals. Since plants and animals are not immortal, and since they survive the hazards of attack by adverse influences sufficiently to be extremely numerous on the earth, it follows that their excretions and their dead bodies or parts of them are important minor habitats in themselves. This can be illustrated by reference to the examples of tree holes, logs and other dead wood, leaf litter, fungi, sea wrack and carrion.

Here something may be said about the relation of vegetation to animal life in general. It is well known from general observation that vegetation bulks much larger than animal life, in other words, that animals do not succeed normally in eating the vegetation at all completely. As A. H. Church wrote in 1922: 'Trees or grass clothe the visible surface of the land, in close canopy or as thick undergrowth; animal life, beyond a few birds and the animals maintained by man, is conspicuously inconspicuous... The living plant... is dominant in aggregate mass and volume of living material...' There are occasional or even recurrent instances where the balance of a community is so completely upset, or fluctuates so far outside its normal range, that vegetation is destroyed. Two rather common

ones are the defoliation of oak in this country by caterpillars, and similarly of conifers in Europe. How far this is a natural event, or is due to human alteration of primeval conditions, we cannot be certain. We do know, however, that the interference of man with predator populations and other means of protection of wild deer have brought about a series of large-scale crises in forestry, especially in the United States (Rasmussen, 1941; Leopold, Sowlis & Spencer, 1947). I think we may suppose, for a working theory, that the interrelations of animals in a community impose checks and controls which normally prevent the herbivores from reaching a starvation level and destroying vegetation, though their fluctuation may cause considerable periodic starvation among predators. These controls may be both intraspecific and interspecific. Anyhow, the great surviving predominance of vegetation and the mortality of plants means that a very large production of dead plant matter in various forms is going on everywhere. This is partly produced seasonally, as with leaf litter, partly all the year round, as with wind-blown branches and fallen trees. Some whole great ecosystems, like lake and sea abyssal zones, depend on dead plant (and animal) matter.

One interesting minor habitat, widely developed in all forest regions, is *the small tree hole full of water*. It depends primarily on tree structure, but usually also on decay, which proceeds in damp conditions. The tree-hole mosquitoes are the most interesting members of this fauna. There are three British species. Other insects also occur, and Keilin (1927, 1932) has made some study of them. The most complete ecological survey is an American one, by Jenkins & Carpenter (1946), who found the same three genera of mosquito, as well as a fourth, that has turned carnivore on the others. They noted also a midge larva and two other species of flies and several beetle larvae, together with a microfauna formed by *Cyclops*, a nematode worm, rotifers, and several Protozoa. Tree-hole mosquitoes are extremely important in the Tropics in connexion with several diseases, including yellow fever.

Log succession, which is a very large subject in itself, can only be dealt with briefly. In a forest glade log formation often results from the death of a tree, and perhaps later of other marginal trees which become exposed to wind forces they were not bred to resist. If the logs and fallen branches come down fresh at the right season, they form the focus for an intense activity of animals specially adapted to invade and exploit this minor habitat at different stages of its decay. At the same time, stumps or broken trunks, sometimes whole dead trees, may remain standing for some years, and these have a rather different invertebrate faunal composition from logs, and such dead trunks are also used both for feeding and nesting by such birds as woodpeckers. Here is a very important element, not only in the woodland life pattern, but in the cycle of decay and humus formation. The most thorough ecological study of logs from a modern point of view is by Savely (1939), in North Carolina, where he made exhaustive collections of insects from oak and pine logs, over some years, and worked out also part of the story of their food habits as well as the microclimates of the logs. In the pine logs he found ninety-five species during the first year, i.e. on fresh logs. First came twenty-two species of phloem-feeders, like bark-beetles, and their galleries were invaded by thirty-seven kinds of saprophagous and fungus-eating forms. There were twenty-nine kinds of predators, nine parasite species, but only four sapwood-feeders. By the second year the phloem-eaters had gone, indeed, they were only present for the first few months. The total numbers of all insect species in the second to fourth years, were sixty-seven, fifty and thirty-five. After that the logs began to drop to bits. The oak species were rather fewer, and to a large extent different.

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Hanson (1937) gives a full description of the animal community around the pine bark-beetle (*Myelophilus piniperda*) in this country. These included parasitic nematodes, eleven species of parasitic Hymenoptera, twenty-seven predatory beetles or their larvae, *Rhaphidia* (a predatory Megalopteran), five predatory fly larvae, and birds (though the last were not quantitatively important). I have (1948) been breeding out the fauna linked with the ash bark-beetle (*Hylesinus fraxini*). In only one 8 ft. length of log, I have found, besides thousands of the bark-beetles, one or two species of other larval beetles, a gall-fly, several kinds of Anthocorid bug predators, more than six parasites, mostly Chalcids (including a small hyperparasite), and a very abundant population of Uropodid mite that arrives attached to the parent beetles, and leaves in a similar manner.

Another group of beetles, the longicorns, is important in penetrating wood. Some excellent work has been done by Kaufmann (1948) in putting together and adding to information about the kinds of dead wood that various British species of this group occur in. It appears that their range is fairly wide and that, while bark-beetles are highly specific to particular kinds of tree, longicorn beetles are often much less so. It remains to be determined how restricted are the fungi in decaying wood and the insects that live on them. I would like here to make a plea to foresters and to conservation people for dead wood to be allowed to follow its fate and lie about. It has been noted that natural forest has an enormous amount of dying and dead wood on the floor, and Jones (1945) has cited interesting figures for the amount of natural dead standing and fallen timber. It would be a great pity if ideas of tidiness derived from farm management, from purely traditional silvicultural ideas, or from town life, should lead to the constant removal of dead and dying wood from forests. There is undoubtedly a very large number of insects that depend for their survival directly on this minor habitat of dead and dying wood either on the tree or lying on the ground. Among them are some of the most exciting, large and beautiful or rare members of the British fauna. One need only mention the stag-beetle, the longicorns, a good many click-beetles, and several ants (like *Lasius brunneus*) that in turn have attached to them rare species of myrmecophiles. There are many more. Furthermore, logs and dead branches form the night or day or seasonal refuges for some woodland animals. In a short day's collecting on logs of various ages with a class of students last year, we found queens of two species of wasp, queen bumble bees, large Carabid beetles, ichneumons, and, in addition, found that some of the larger slugs and snails take refuge under logs, from which they forage over the litter when conditions are favourable. Can any forest entomologist or ecologist prove that the clearing away of at any rate fallen deciduous dead wood is necessary in the interests of forest health?

To emphasize at this point the large role played by minor secondary habitats in the animal community, the remarkable survey that Donisthorpe (1939) did over many years, in the Windsor Forest area, should again be mentioned. He collected about 1870 species of beetles (almost exactly half of the British beetle fauna), many of them again and again, and in every case he noted the exact minor habitat. This report forms the most important body of raw facts about this phase of ecology for Britain, although it has limitations from inevitable lack of quantitative data, and from the absence very often of any indication of the major habitat, except in so far as it can be inferred. About 285 species were collected under bark, in decaying wood, and in wood frass, and similar minor habitats, and most of these are species known to live there normally; about 270 species (some the same as those in rotten wood) occurred *in fungi*, some of which (mostly the conspicuous tree or log

bracket forms) are named. In another paper Donisthorpe (1935) has given a list of 115 truly fungus-living British beetles, together with records of their host species. For example, *Polyporus squamosus* ('Dryad's saddle') has thirty-five species, *P. sulphureus* ('Sulphur bracket') thirty-nine, *P. betulinus* ('Birch bracket') thirty-six, *Pleurotus ostreatus* ('Oyster mushrooms') nineteen and *Fomes fomentarius* ('Tinder bracket') sixteen. But by no means all these were exclusive to any one species of fungus. One family, the Cissidae, is practically confined to toadstools growing on tree stumps, etc. He lists also a further thirty-three beetle species that have been commonly found in fungi, though their habitat range is much wider.

There is no doubt that a very substantial part of our British beetles occur in decaying matter or in fungi associated with it, and less than a third are herbivorous on green plants. There is a similar division inside the flies, though one cannot say exactly what the ratio is; but the number of saprophagous forms is very large, including such groups as mosquitoes, Mycetophilid flies and many small families. A substantial number of Collembola, Thysanura and aquatic insect larvae, many of the Mollusca, the earthworms, most of the woodlice, some aquatic Crustacea, and many millipedes, mites and nematodes are in the same category. And their habitats are frequently discrete units scattered over an area, though it still remains a major query how far soil animals are distributed in a patchy or discontinuous manner. The same query applies to *leaf litter*, though anyone who has observed the floor of a mixed wood in autumn cannot fail to note the patchiness of different leaf litters as from beech, oak and other trees and shrubs, as well as from herbs and grasses. The patchy distribution of ground mosses is to some extent the mirror image of the pattern of the heavier leaf litter areas.

It is at present impossible to give a clear distinction between those dead wood species of animals that actually eat wood, and those that depend on fungi. The same thing applies partly with nest species. But when we consider Donisthorpe's records, and the fact that there are several thousand species of macroscopic fungi that may serve as habitats—indeed, one can find beetles of fly larvae frequently in almost any ageing toadstool population that one slits open at the right season—it is clear that they also form one of the most important minor habitats. A beginning has been made in studying the animal relations to microscopic fungi, as in the family Lathridiidae among the beetles, some of which have been cultured successfully on *Penicillium* moulds (Hinton, 1945), and which are frequently found in odd places like under bark and in old wasp nests. Perhaps we may eventually have ecological survey lists that give all the fungi in detail by species, and mention at the bottom just 'Phanerogams and mosses also present'.

There are other minor habitat centres in decaying plants, for instance, dead bramble (whose stems are famous nest sites for small wasps); and also on the seashore, where there is a specific *wrack fauna*, that has been worked out in great detail by Backlund (1945) for the Baltic. He found 108 species as regular inhabitants, of which about a third were restricted to wrack.

Dead wood and leaves are 'plant carrion'. *Animal carrion* adds a still further note of variety to every community. Donisthorpe (1939) recorded ninety-five species from dead animals and birds and from old bones in Windsor Forest area—that is, of course, only a sample of the British carrion fauna. The only published attempt to describe a carrion community in full ecological terms is that of Fuller (1934) in Australia. She examined the succession communities of insects invading carcasses of sheep. This survey disclosed

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forty-one species of flies, belonging to fourteen families, the most important ones being the bluebottles. Of beetles there were twenty-eight species belonging to ten families, and in addition seven parasitic Hymenoptera—a total of seventy-nine species, of which twenty-three were quantitatively or ecologically important. There was succession according to the state of the carcass, and the seasonal temperature, and some remarkable competition phenomena were observed, in which saprophytic fly populations of different species were also predatory upon one another.

Some of the chief minor habitats which form the focusing points for special animal communities have now been mentioned. In doing so I have emphasized the frequency of discontinuity, and the relatively small sizes of the populations. This really needs qualifying in several ways. There must exist a number of populations which are spread out less discontinuously, either because the basic habitat that I have been calling 'minor' is major in extent, or because the range and type of activity and movements of some species is not limited very much by the minor patterning. And it is clear that exact regularity of pattern, though interesting where it occurs, and convenient in certain ways for study, is of less fundamental significance than the occurrence of discontinuity as such.

So far, except for mentioning some of the ecological succession that occurs in minor habitats, the whole pattern had been described as though it were a static arrangement, or at any rate an instantaneous picture of a moving one. It has been noted that mathematical theories about populations have mostly treated them as if they were randomly interspersed over the area of some major habitat (imagined to be in some sense uniform), whereas we have seen that there are groupings of populations around small centres dispersed through the habitat, partly in regular patterns, and partly not; some related in their distribution—as might be logs and the occurrence of glade-living herbs and shrubs in a wood—and some quite independent, as with the territorial arrangements of owls relative, say, to the distribution of societies of *Adoxa* or clumps of wayfaring tree in a wood. Or again there may be a relation between the centre of an animal or bird's territory (as with squirrels' or sparrow hawks' nests in trees), but little or none to the frequency distribution of plant species in the territory chosen for hunting.

Until we know more about the type and scale and distribution and relationships of these minor communities, we can hardly expect to understand very much about the dynamic relations. But one may with advantage explore a few general ideas. These come under the headings of population control within any one minor community; vertical and lateral movements of populations; the dynamic relations between minor community units of the same kind; those between minor communities of different kinds; and oscillations in numbers.

The *dynamic balance within small communities* like dung and carrion has been studied, but not with such quantitative care as to throw much light on the exact mechanisms of control. As regards control, we must distinguish very sharply between communities of animals depending upon living plants, or other animals and those depending upon dying or dead plants and animals. We already know as a general fact of observation that plant populations usually maintain themselves in spite of the inroads upon their biomass made by animal populations. Indeed, so apparent is this that it has been for many years a convention among botanists to treat dynamic vegetation systems as though the animals were not having any influence upon the energetics of the plants at all; or only to bring this idea in where the inroads are of a very conspicuous kind, as with rabbit or stock or deer grazing. But a little reflection will show that every plant population (except those few that

are, like many of our alien garden forms, free from attack) must be losing a definite and ascertainable amount of energy to the animals they support. For some curious reason, this is usually only studied when the plant is of economic importance, and often then only when attacks are severe and noticeable. Of course, exactly the same reasoning applies to animals, which are liable to attack or some energy drain from parasites. Thomas Park's recent experiments (1948) with the flour beetles *Tribolium confusum* and *castaneum* afford one of the most convincing demonstrations of this principle. In laboratory cultures, he was able so to control conditions that competition between the two species could be measured, and the results determined within a certain rather broad degree of probability. When both species were infested, as they usually are, with a Sporozoan parasite, *Adelina*, species A usually (though not always) replaced species B in competition experiments, but when the parasite was eliminated from cultures of the beetle, species B usually (but not always) eliminated species A. Has anyone yet measured the loss of potential energy to a plant species, from the operations of its herbivorous fauna, and the possible effects of this upon competition? I think the principle has been shown with differential rabbit grazing; but it must apply almost universally. This is to say, that competition hardly ever takes place between 'pure cultures' of plant species, uninfluenced by the animal community dependent upon them. But we may reasonably suppose that only those species or associations of plants will survive in evolution which carry animal communities that do not, either through the resistance or vitality of the plants themselves or by the internal controlling factors in the animal community, get completely devoured, or at any rate so weakened that they cannot compete successfully.

But with waste material like dead wood, litter and carrion, there is no reason at all why the animal community should not devour and destroy its habitat or the resources in it completely, provided enough of these temporary supplies are being produced (as with cattle dung) in relation to the life length and other properties of the animals living in them.

Varley's quantitative study (1947) of the insect fauna (nine herbivores, fifteen parasitic Hymenoptera and one predatory fly) living in a population of knapweed (*Centaurea nemoralis*) flower and seed heads, is the only one done so far that throws much light on the inner workings of a small community dependent on plants, of which the different micro-units are in dynamic relationship. His work was directed to some very interesting questions about host-parasite balance. But I think the other important conclusion coming out of it, apart from showing the inherent complexity of even a small fragment of the animal community, was his demonstration that among an apparently complex network of food relationships only five were really significant in controlling the numbers of the central species, the knapweed gall-fly (*Urophora jaceana*). May we pray that similar simplification will emerge from other studies of the sort!

The degree of *interchange between minor communities* is obviously a very fruitful subject for study, because it will greatly influence the behaviour of the whole population, and also has a bearing upon modern theories of evolution, such as those of Sewall Wright. It is, however, linked up with the wider question of patchiness in populations, which can be brought about in several ways: (1) patchiness may be due to the separation of minor habitats in a more or less repeated pattern throughout some major habitat; (2) patchiness may also occur entirely through the interaction of plants and animals on their habitat and on each other: this seems to happen in marine and perhaps in fresh-water plankton;

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(3) it can also be caused by the short-term oscillations, or (4) by long-term scarcity of a species. I realize that the populations of any minor unit are never exactly the same as the others; this point has forcibly been brought out by Diver (1934, 1938), in his Studland Heath survey. Nevertheless, we must admit that there is a substantial amount of general basic resemblance between one dead rabbit and another, or between different oak trees or wood-ant nests. The differences arise more often through the varying species composition of the communities, and these may be due not so much to basic differences in the habitats (apart from seasonal ones) as to the improbability of all the species that could live there finding that patch, or arriving in time to colonize it at the right stage, or succeeding in establishing a population there. This part of the subject has been discussed and analysed a great deal by botanists, but I do not know of any very relevant work on animals. But once we admit that the composition of the colonists will vary greatly with chance, we must see that the resulting species interactions (e.g. through competition or predation) will work themselves out in a number of different solutions. In other words, we shall expect to find minor habitat centres differing rather strikingly in their faunas, and seldom to be able to do more than express a probability or possibility that a given list of species will occur. I think it is even conceivable that the existence of certain scarcer species in such minor community units depends partly on stronger competitors being absent by chance. These considerations make it even more difficult to attach very real meanings to the mean densities of populations spread over wide areas, since they will always tend to be split into numerous small components that are living in different biotic environments. The whole subject of interchange by population movements between isolated minor habitats requires extensive study by marking methods.

One of the very interesting features of these small habitat units is that *many species spend alternate parts of their lives in more than one* of them. Thus longicorn beetles live in dying or dead wood, and many of them as adults visit flowers of herbs or shrubs or trees and presumably feed on pollen. *Strangalia (Leptura) maculata*, that breeds chiefly in dead birch wood, but also in that of several other broad-leaved trees, is commonly seen on such flowers as the meadow-sweet (*Spiraea ulmaria*), and the blossoms of bramble, again, with a fairly wide range of choice in species of plant. The chief thing uniting larval and adult host-plants is that they are mostly species of woodland openings. Blackman (1918) gives a long list of *Leptura* species and other longicorns visiting *Spiraea* and blackberry flowers in an American locality. About half the British longicorn species are known to have a flower-visiting habit (Fowler, 1890).

Similarly, some dung-feeding flies haunt other habitats. The predacious fly (*Scatophaga stercoraria*) so abundantly seen on cowpats, does much of its hunting on hedgerows and scrub (Dr B. M. Hobby, personal communication). *Hydrotaea irritans*, that fly that is such a nuisance to us in the summer woods, is common in cattle dung, and it may originally perhaps have bred on wild cattle when glades were a small feature in a woodland landscape; whereas now the glades have become huge pasture-field areas with scattered woods between. But it still enters woods in large numbers.

I have similarly observed green-bottles of the genus *Orthellia*, that breed partly in cowdung in the fields, entering neighbouring woods and haunting willow blossoms in the spring.

I think it stands to reason that the inhabitants of minor habitats that are separated from one another by some distance should wander in search of new patches, especially as so

many of these are temporary. It is also natural that we should find them feeding on flowers or honeydew of trees, or congregating at certain points for mating. And evidently in many cases this alternation of minor habitat during the life history has become obligatory. Among insects, e.g. some aphids, there are instances of alternation between two plant hosts during the life cycle which involve similar migrations. And we may consider that the tree canopy or trunk, and the soil beneath, are similarly different minor habitat units separated in the vertical plane.

In order to make such migrations in search of new places or resources, an animal must have sufficient energy stored up to make the journey, unless it can find refuelling stations en route. Williams, Barness & Sawyer (1943) did an ingenious experiment on *Drosophila funebris* that illustrates this point. They attached each fly by wax at its tail end to a wire in such a way that it could use its wings as if in flight, but could not escape. They found that a week-old fly died on the average after 110 min., during which time it had made over a million wing-beats, and that it had used up all the available glycogen in its body. Very young and old flies died in about 20 min. We should expect therefore to find some relation between the migrating power of animals and the distance between minor habitat units. We shall not be surprised to find in the records of a single species, a great deal of apparent mingling of minor habitats, though further analysis might explain them quite simply.

I have only alluded in a very slight way to some of the dynamic implications of the types of population interspersal pattern that occur in nature. These small patterns are in turn built up into larger ones, such as one sees between wood and field and river, and there is much interchange of fauna between these. And on a still larger scale we have the alternation of bird life between England and Africa, or Norway and England, which expresses the same principle.

The patchiness of habitats affects *oscillations in numbers*. It is becoming increasingly understood by population ecologists that the control of populations, i.e. ultimate upper and lower limits set to increase, is brought about by density-dependent factors, either within the species or between species (see Solomon, 1949). The chief density-dependent factors are intraspecific competition for resources, space or prestige; and interspecific competition, predators or parasites; with other factors affecting the exact intensity and level of operation of these processes. This is another way of saying that control of numbers, and therefore of much of the oscillation that takes place in populations, depends on community relationships. It is therefore interesting to inquire how the splitting up of populations into partly isolated units affects these mechanisms. A good deal is beginning to be written about this, more especially in connexion with the development and natural control of insect outbreaks. Nicholson & Bailey (1935), whose main theory deduces that under certain conditions predator-prey or host-parasite population oscillations will tend to get more and more violent until they result in local extinction, have suggested that this might occur in nature, but that because it is happening in different population units, and not necessarily simultaneously, lateral migration is always replacing the extinguished or shortly to be extinguished nuclei. I find this theory, which has also been discussed by Smith (1939), rather difficult to believe in its entirety. But it is at any rate well known, and can be seen in the field, that outbreaks such as those of the oak moths do not affect every tree equally, and one may see immune trees in a devastated wood, and such trees form a reservoir of populations that have been almost

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wiped out elsewhere—a consideration applying both to the moths and their complex, but also to the rest of the fauna which suffers from the defoliation.

From this analysis there begins to be seen an ecosystem on any area composed of comparatively limited minor centres of action, each having certain distinctive characteristics as habitat that are reflected in their communities, and which have a considerable amount of interchange by lateral and vertical movements. One would like to see a large number of studies by ecologists and by naturalists on these small component communities, but carried out in such a way that the data can eventually be linked with similar studies. In this way there might emerge some more clear-cut general picture of the workings of different major ecosystems. It has often been said to me by specialists that the time is not ripe for integration of ecological data into community form, with the implication, rather comfortable for the specialist, that there is no need to do anything about the synecology of animals or of animals plus plants in our lifetimes. I disagree with this outlook. Suppose you were in an engineering department that was faced with wiring for telephones a city with half a million houses. You would not say that because there is not enough wire and instruments to do the whole lot at once that you would have to wait ten years until they were all available. You would start a few centres and fit up as much as possible, but leave a great many terminals and some whole exchanges unconnected, and many houses without communication to the centre, but link them up as material came along later.

The analogy with community research on animals is very close. What has been deficient so far in most of the smaller detailed records, or surveys of minor groupings, is that they have not been recorded in a way which would permit of later linking with other surveys; the habitat data have often been ludicrously sparse, the context lacking, and the information incapable of full use by ecologists. This is shown almost wherever one looks for habitat data for animals. Even a first-rate survey for one animal group of minor and microhabitats like Donisthorpe's usually lacks any definition of the major habitat. 'In fungi' by itself is a small part of what we need. Similarly, 'the white admiral butterfly lays its eggs on the honeysuckle' does not tell one the additional vital fact that this occurs usually in glade or ride conditions and not under thick canopy. Nor for that matter does 'honeysuckle f.' in an oakwood necessarily tell one that part of its population is non-flowering and has probably been brought there by birds eating berries on the more open parts of the wood.

We require, therefore, two things to improve the recording and use of the vast detailed knowledge that is being collected all the time about wild animals (and plants). First some general notions about patterns of habitat and population interspersions, i.e. the context into which such observations fit. That I have tried to indicate in this paper in a very condensed form, but it really needs an enormous amount of further study and thought. Ecologists, and especially animal ecologists, need some comprehensive principles for classifying habitats, based on these patterns and their component parts. We need a *Systema Naturae* for habitats of all sizes, and we have arrived at a stage of knowledge where the outline of such a system might be drawn up. This time it cannot be done by one man—it would require a great deal of co-operative effort. The British Ecological Society might very well consider it worth while to spend some effort in trying to draft one, so that the present fragmented records could fit into a general synthesis of data, even though that synthesis may take many years to accomplish. But it might help to do for ecology what Linnaeus did for taxonomy. As with taxonomy, the categories set up would often be only approximations to reality, but they would if properly designed in the light of general dynamic

principles, provide a much better method of organizing field data than we have at present. And it might form an extra sheet anchor for naturalists, who may feel that much of ecology is becoming purely quantitative, abstract and mysterious. I hope, however, that we shall not invent fantastic Greek names for these categories, but use good old English terms like tree, tussock, dung and carrion. Later, when we begin to feel some assurance that the classification has been compared with ideas from other countries and begins to have a general validity, it might be necessary to invent more of an international lingo for the component parts.

As a first and very simple approach towards this ideal, I would mention the type of record card that has been in use for several years at Oxford, in connexion with ecological surveys, and which has begun to provide valuable habitat data for animals.

Species:

Place:

Wytham Woods, Berks.

Date:

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Time (G.M.T.):

Habitat: Major:

Minor (e.g. plant):

Micro:

Vertical:

Observer:

Specimen code letter:

Please label specimens with your Initials, Date and Code Letter, e.g. C.D. 1. 5. 47 (A).

The record on any one card is meant to cover what may be called a single ecological 'incident' or significance. Such molecular information does not compete with intensive studies by research ecologists or naturalists, but supplements them. Here I would just say a word about the terms 'professional' and 'amateur' which one frequently hears used in a contrasted manner. Those who study ecology are not all professional ecologists, because that does imply certain special critical standards and experiences of methods; but are we not all amateurs in some respect? Our subject-matter is so wide that it includes vast outer fringes with which we have only an amateur acquaintance. This is true of nearly all scientific research, but of ecology par excellence. I would illustrate the point by a story. Several years ago I happened to find a live population of the pointed snail (*Clausilia rolfhii*), a species thought to be quite extinct in the Oxford region. I took it for confirmation to a friend who is naturalist and taxonomist of very considerable skill. He said: 'You know, you amateurs have all the luck.' And, observing a faint surprise on my face, added, 'If you know what I mean.' I *did* know what he meant, and the point of the story is emphasized when I add that the professional in this instance is a professor of theology.

There is no doubt that all ecologists are seeing things, and quite often recording them, if only in their notebooks, that could be valuable additions to our general accumulating knowledge of communities, if they were made in the form I suggest. This suggestion, of course, does imply the existence of active centres at which the data will be accumulated and eventually used scientifically. What better one can be imagined than the new Nature Conservancy, and any associated research institutes that it may develop?

The relation of such recording work to a real appreciation of the dynamic implications of habitat patterning may be illustrated by an example. Suppose one records, with date

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and time and place, the Chrysomelid beetle *Galerucella viburni* feeding, at a height of 3–5 ft., upon the upper side of leaves of the wayfaring tree, *Viburnum opulus*, in a ride in an oak-ash-sycamore woodland on limestone. That is a reasonably good primary record of an ecological incident. But suppose I put it in more general terms, for interpretation. 'I have observed an unknown number of active parcels of potential energy of unknown size, moving about in a manner that may be random or not, in a habitat that I can only describe by some rough indicator species of plants and the underlying rock. I assume that because these parcels are probably morphologically similar they are also more or less genetically similar. The patch of habitat in which they were operating was one of an unknown number of similar and some quite dissimilar ones situated at an unknown distance from this one. The operations of these parcels of potential energy is likely to be interrupted or reduced by the activities of others: I do not know what these are in Britain, but I can cite some suggestive data from Europe.' In this way one may arrive at a constructive ignorance—insight not too damped by caution.

It can be seen that population interspersions is a subject that involves equally all the present theories of demology as well as the arrangement of communities, because it is of the nature of animal communities and therefore of their populations not to be evenly distributed, though the unevenness of density is itself subject to ecological laws.

Dr Watt ended his Presidential Address with a quotation from Shakespeare about the relation of the part to the whole. I will venture to end also with a quotation, from a little-known sonnet-writer (J. B. White), which might be applied to minor communities and habitats:

Or who could find,
Whilst fly and leaf and insect stood revealed,
That to such countless orbs that mad'st us blind?

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SOME CHEMICAL ASPECTS OF A PEAT PROFILE

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In recent years much attention has been focused on the stratigraphy of peat bogs. However, in contrast, there has been much less work on the chemical characteristics of the various layers. This paper is a preliminary study of certain features of the chemical stratification, particularly of elements figuring in the base-exchange complex. While it is not possible at this time to explain all the data presented, they are perhaps of sufficient interest to be placed on record. It is hoped that the work may be continued at a later date.

METHODS

The peat profile studied is located at Striber's Moss, on the Leven estuary in North Lancashire and south of Windermere. Samples were taken on 26 August 1948 with a peat borer. They were transferred to the laboratory allowing the least possible access of air to the parts used in analysis. The analyses were carried out within the next week. The order and method of analysis is as follows:

pH. Glass electrode on fresh sample.

Conductivity. Determined at 25° C. using the apparatus of Mortimer (1942). It should be noted that the value given is that for the fresh peat and not that for interstitial water.

Redox potential. Platinum electrode, after an interval of one day allowed for steadying. The conditions in the peat were believed to be air-free.

Fresh Water and Humus, dry (at 100° C.) and ash (at 500–550° C.) weights.

Exchangeable base and exchangeable hydrogen. Done on the fresh peat and therefore including water soluble components, following the method of Brown (1943).

Ash-alkalinity. Ash taken up in 0.1 N-HCl and back-titrated with mixed indicator (methyl red and bromcresol green in alcohol).

Calcium. On the alkalinity solution after two days, by the picrolonate method as used at the Freshwater Biological Station, Wray Castle.

Iron. Thiocyanate method on acid solution of ash.

Ammonia. Micro-Kjeldahl distillation of the exchangeable base solution.

DESCRIPTION OF STRIBER'S MOSS

This moss is a raised bog partly invaded by pine and birch. It is being cut at one end, and in some parts has suffered from burning. The samples were taken from a relatively undisturbed site where the vegetation is as follows:

Abundant	Frequent
<i>Sphagnum papillosum</i>	<i>Cladonia sylvatica</i>
<i>Eriophorum vaginatum</i>	<i>C. uncialis</i>
<i>Scirpus caespitosus</i>	<i>Sphagnum plumulosum</i>
	<i>Rhynchospora alba</i>
	<i>Eriophorum angustifolium</i>
	<i>Narthecium ossifragum</i>
	<i>Erica tetralix</i>
	<i>Calluna vulgaris</i>
	<i>Andromeda polifolia</i>

While detailed stratigraphy may be very complex, it is sufficient here to recognize the three main layers of peat, originally recognized in these Lonsdale 'mosses' by W. M. Rankin (see Tansley, 1911). Immediately above the basal grey clay is a layer of fen peat approximately 1.5 m. thick, grading from probably pure *Phragmites* at the bottom to a mixture with *Cladium*, *Menyanthes*, *Equisetum*, *Carices* and willow carr species at the top. Next comes a stratum of dark-brown peat with *Eriophorum vaginatum* very abundant and the much oxidized remains of *Sphagnum*, representing the earlier phase of bog growth. Towards the top of such a zone a 'Grenzhorizont' is generally found and this is thought to be at about 3.2 m. in the profile studied. The top layer consists chiefly of originally 'grey' *Sphagnum* peat with some admixture of cotton-grass and ericoid species and is about 3 m. in thickness. Drainage and marginal cutting have resulted in this layer being browner and more oxidized than formerly. Samples of these layers were taken down to the basal clay as follows:

- (1) 0-0.5 m. Red-brown *Sphagnum* peat with *Eriophorum vaginatum*.
- (2) 1.0-1.5 m. *Sphagnum* with *Eriophorum* rootlets and some heather.
- (3) 2.0-2.5 m. Mostly *Sphagnum* with ericoid remains in a layer at 2.25 m.
- (4) 2.5-3.0 m. *Sphagnum* with occasional *Eriophorum* and heather.
- (5) 3.0-3.5 m. More fibrous and darker, with more *Eriophorum* (both spp.). *E. vaginatum* in bottom half.
- (6) 3.2-3.5 m. *E. vaginatum* plentiful.
- (7) 3.7-4.0 m. *E. vaginatum* very abundant.
- (8) 4.0-4.5 m. Mixed fen and carr peat.
- (9) 5.0-5.5 m. Fen peat with *Phragmites* becoming a mat at the bottom.
- (10) 5.5-6.0 m. Grey clay with roots in upper part.

It should be noted that the samples, especially no. 5 and to some extent no. 6, contain peat of different vegetational origin, so that some variation in results may be expected. Mixing was not desirable as it was certain to allow oxidation which affects certain exchange properties to a marked degree.

Since the volume/weight ratios are not known it is difficult to compare the clay with the peats above. However, the clay results are given to complete the picture.

Table 1. Results

Peat type	Sample no.	Depth (m.)	pH glass	Conductivity (mho $\times 1000$)	Po'tential at pH 5 (E_s in mV.)		Water (% dry wt.)	Ash (% dry wt.)	Alkalinity (m.equiv. % dry wt.)	Exch. base (m.equiv. % dry wt.)	Exch. hydrogen (m.equiv. % dry wt.)	Calcium (mg. atoms % dry wt.)	Iron (mg. atoms % dry wt.)	Ammonia (mg. atoms % dry wt.)
					0	30 min.								
<i>Sphagnum</i>	1	0-0-0.5	3.84	9.3	43	207	2200	4.7	12	26	61	4.4	3.0	0.8
	2	1.0-1.5	4.19	8.6	91	230	1800	3.6	35	26	60	3.2	1.6	1.3
	3	2.0-2.5	4.49	9.9	—	—	1700	2.1	43	32	56	2.5	1.0	2.1
	4	2.5-3.0	4.49	10.5	—	—	1500	1.7	26	30	58	3.8	1.1	1.7
Transitional	5	3.0-3.5	4.62	9.6	366	228	1600	1.6	19	26	53	3.3	0.8	1.8
<i>Eriophorum</i>	6	3.2-3.5	4.44	9.3	456	458	1300	2.0	20	26	46	3.0	1.5	1.5
	7	3.7-4.0	4.45	9.2	448	383	1200	2.0	20	32	62	4.0	1.9	2.0
Carr and fen	8	4.0-4.5	4.83	11.9	346	344	1300	2.0	15	29	54	8.0	3.4	1.7
Fen	9	5.0-5.5	4.83	11.8	329	306	1100	4.7	23	49	50	15.5	9.7	2.0
Clay	10	5.5-6.0	6.08	16.9	373	329	70	94.6	83	46	18	52.0	41.7	0.4

Water and ash contents

The water content of the peats decreases with depth and falls noticeably in the layer of *Eriophorum vaginatum* which is rather fibrous. Ash drops steadily through the *Sphagnum* peats, rises in the *Eriophorum vaginatum* zone and then continues to increase in the fen layer.

It is not known what elements contribute to the high ash contents of the peats at the two ends of the profile. Alkalinity is low at the highest range of ash content, and the surface layer is also rather low in calcium and iron. From the analyses of Misra (1938), silicon suggests itself as likely to be abundant in the fen peats. It may also be present at the surface in some quantity if the moss has been burnt.

Conductivity and pH

The general tendency is for both values to increase with depth, suggesting greater decomposition and a larger percentage of water soluble bases in the lower peats. Here again the *E. vaginatum* layer is distinctly delimited and shows lower values than the general trends. This species seems very slowly decomposed, its tufted nature being long recognizable.

Exchangeable ions

There appears to be little correlation here with results from other analyses. Exchangeable hydrogen tends to decrease with depth and exchangeable base to rise, especially in the deepest layer. However, the picture in the *E. vaginatum* zone is difficult to interpret, a drop in both exchangeable base and hydrogen occurring in the upper layer and a distinct increase in the lower. The lack of uniformity of these samples at this level or oxidation effects may be responsible for the discrepancy. Exchangeable ammonia tends in general to follow total exchangeable bases.

Calcium, iron and ash-alkalinity

Both calcium and iron at first decrease slightly with depth, possibly due to plant uptake causing surface concentration. There is then a rather marked increase in the fen peat. On the other hand, ash-alkalinity reaches a maximum at 2.25 m., after which it decreases, though a slight increase occurs in the lower fen peat. It is not known which element is responsible for this maximum of ash-alkalinity in the *Sphagnum* peat, but Mattson and his associates (1944-5) find magnesium replacing calcium in the exchangeable base of bog peats at similar levels. It may be that the bog plants take up magnesium in preference to calcium since they contain large amounts of fatty substances which the latter would immobilize (Hinchliff & Priestley, 1924). The decrease in alkalinity toward the present surface is perhaps due to the locking-up of the contributing element in decay-resistant compounds at the depths to which roots could penetrate. This view is supported by the fact that the exchangeable base does not rise equally sharply in this region and from the data of Mattson, Sandberg & Terning (1944-5) it is seen that the calcium/magnesium ratio in the exchangeable base tends to increase in the upper layers of the 'grey' *Sphagnum* peat.

Calcium calculated as milliequivalents exceeds alkalinity at certain points. It is believed that there was perhaps some formation of calcium sulphate on ashing and its slow solution in the two-day interval between the determinations would account for the differences. Exchangeable base also exceeds alkalinity at some levels, probably due both to the formation of calcium sulphate in the ash and to the presence of iron and possibly manganese in the reduced state in certain layers. Ammonia is present in the exchangeable base (see

Table 1) to the extent of about 2 m.equiv. percentage dry weight. It is less at the surface, presumably due to plant uptake.

Redox potential and calcium/iron ratio

It is these results which are perhaps the most interesting. The uppermost layers are rather strongly reducing. The fen peats are just on the border line, while the *Eriophorum vaginatum* zone, with an E_h (Pearsall, 1938a) of 350–500, appears to be definitely oxidizing. Since there is apparently very little possibility of oxygen being present at this depth, the potential seems to be due to the structural characters of the peat itself. Pearsall (1938b) finds that the surface of bogs with a cover of *E. vaginatum* may be feebly oxidizing in contrast to the reducing surface of *Sphagnum* bogs, although he suggests that this may be due to air channels in the roots.

The difference in potential is further manifested in the state of the iron present. In testing the acetic acid solution of exchangeable base by the modified thiocyanate method of Comber (Misra, 1938) it was found that a deep colour was given in sample no. 2 on addition of hydrogen peroxide. This indicates the presence of ferrous iron. On the other hand, peroxide had no effect on sample no. 6 from the *Eriophorum vaginatum* zone, showing that iron is present in this peat in the ferric state and has not entered the base exchange complex.

It is also interesting to consider the calcium/iron ratio. The trend is for a low value at both surface and depth, with a maximum in the deepest layer of *Sphagnum*. The *Eriophorum vaginatum* zone shows a relative increase in iron over the mixed fen peat, perhaps due to the oxidation of transported ferrous iron to the less mobile ferric state. The subsequent marked increase of the calcium/iron ratio in the *Sphagnum* peat may be due to the plants' inability to assimilate this oxidized iron.

SUMMARY

A study has been made of some elements and chemical properties figuring in the exchange complex of a peat profile. Some of the variations may well be related to those in the vegetational composition of the peats, for a sequence of plant communities of very different character has occupied the site as distance from the mineral soil has increased.

I should like to thank Prof. W. H. Pearsall and Mr F. J. Mackereth for much kind assistance and advice, also the Director and staff of the Freshwater Biological Station at Wray Castle for providing facilities to carry out the work.

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SOIL CONDITIONS AND THE GROWTH OF BEECH SEEDLINGS

By J. L. HARLEY, *Department of Botany, University of Oxford*

(*With four Figures in the Text*)

Beech seedlings may show little effect of varying soil factors during their early growth in woodland on account of low light intensity. The experiments here described were designed to provide information upon the relative growth rate of young beech on a range of soils under conditions of adequate illumination. At the same time, the effect of soil condition on their form and on the variation in mycorrhizal infection of their root systems was observed. The experimental period of two years ended in September 1939 and full use of the plant material was never made. The results now briefly presented are merely those obtained from measurements taken up to that time.

The soils used were six in number and of considerable variety. Three were from beech woodland in the Chilterns, the other three were chosen on account of previous observations on the behaviour of young beech upon them. Details of the nature and origin of the soil, together with notes about the behaviour of beech upon them, are given in Table 1.

Table 1. *Soil types used in the experiments*

Serial	Type of soil	Location of sampling	Geological origin	Vegetation at time of sampling	Behaviour of Beech seedlings
1	Garden soil	Botanic Garden, Oxford	—	—	Grew rapidly and vigorously
2	Shallow Renzina	Near Friston, Sussex	Upper middle chalk	Chalk grassland	Transplants in the open grew very poorly
3	Renzina	Chiltern escarpment, near Monks Risborough	Upper chalk	Beech woodland	Seedlings suffer from drought in summer
4	Brown earth non-calc.	Chiltern plateau, near Great Hampden	Clay with flints	Beech woodland	Beech seedlings grow vigorously
5	Degenerate brown earth	Chiltern plateau, near Great Hampden	Clay with flints	Beech woodland	Beech mast germinates but establishment difficult
6	Podsol upper layers <i>A</i> and <i>B</i> non-calc.	Near Walton-on-Thames, Surrey	Bagshot Sand	Oak, birch, Heath	Beech seedlings and transplants exhibit a die-back and take long to establish

The top 12 in. (omitting the layers of undecomposed organic matter, if present) were sampled. Such a sample may be mixed to a considerable degree of uniformity. After mixing, the soils were placed in pots 9 in. in diameter, of which there were forty-five of each soil type, except of soil no. 6, for which there were only thirty. Equal numbers of pots of each soil were distributed at random in each of three rows. All the pots were sunk up to their rims in pea-shingle to prevent lateral loss of water. When it was necessary to water the seedlings, equal amounts of rain water were poured on to the surface of the soil

in each pot. The seedlings, which were one year old when planted, were derived from a single sample of seed grown by the Forestry Commission. They were already infected with mycorrhizal fungi and had developed abundant mycorrhizal sublateral roots. Hence it may be assumed that any differences in intensity of mycorrhizal infection apparent after the end of the experiment may be due to differences in soil condition.

The seedlings were planted in March 1938 and observations were made upon them at approximately monthly intervals until September 1939. They were then lifted and, after the soil had been washed from their roots, detailed observations and measurements were made.

Table 2. *Analyses of soils*

Ca in mg.equiv./kg.: remainder in mg./kg.

Serial no.	...	1	2	3	4	5	6
pH: Capillator		6.9	7.0	7.2	4.6	4.2	4.4
Comparator		7.0	7.4	7.6	5.4	4.8	4.8
Carbonates as carbon		2704	3750	11,780	0	0	0
Available calcium		16.5	16.7	37.4	2.7	2.2	6.9
Total C (excl. CO ₂) wet combustion		19,895	26,335	53,165	21,290	39,985	56,370
Total N (excl. NO ₃ Kjeldahl)		2774	3210	4892	1157	1213	1650
Ratio: Total C/total N		7.17	8.20	10.87	19.97	32.97	34.17
Nitrate formation on incubation		+++	+	++	+	T?	T?
Soil nutrients by Morgan tests:	P	Low	Medium	Medium	Medium	Low	Medium
	Mg	Med.-high	High	High	Low	V. low	Low
	K	High	Medium	Low	Low	Low	Low
	Ca	V. high	V. high	V. high	V. low	V. low	V. low

Table 2 contains the results of soil analysis made at the time of planting. The six soils are divisible into two groups: nos. 1-3 are calcareous, nos. 4-6 are non-calcareous. Those of the first group have a high pH, free calcium carbonate, low carbon/nitrogen ratio and a high concentration of total nitrogen and exchangeable calcium.

Those of the second group had a lower pH, no free calcium carbonate, a higher carbon/nitrogen ratio and a lower concentration of total nitrogen and exchangeable calcium. Of the second group, one soil, no. 4, was intermediate in a number of respects. The range is unfortunately deficient in soils intermediate between the two groups, such as might contain a high concentration of available calcium, yet lacking free calcium carbonate.

GROWTH OF THE SEEDLINGS

The progress of growth in height of the seedlings in each soil is shown in Fig. 1. The growth of all was relatively slow during the first season and faster during the second. There were marked differences in the rate of growth of some of the treatments. The calcareous soil, no. 1, produced a height growth which was consistently greater than all the others. The remaining calcareous soils, nos. 2 and 3, produced seedlings which grew at a similar rate throughout the two seasons. This rate was faster than the rate of growth of seedlings on the non-calcareous soils, nos. 5 and 6 in which, again, height growth was similar. The non-calcareous soil, no. 4, which, as mentioned above, showed some differences from the other acid soils, produced a height growth during the first season which was significantly greater ($p > 0.05$) than all the other soils except no. 1. This difference between it and the other non-calcareous soils was still apparent in the June of the second season, but

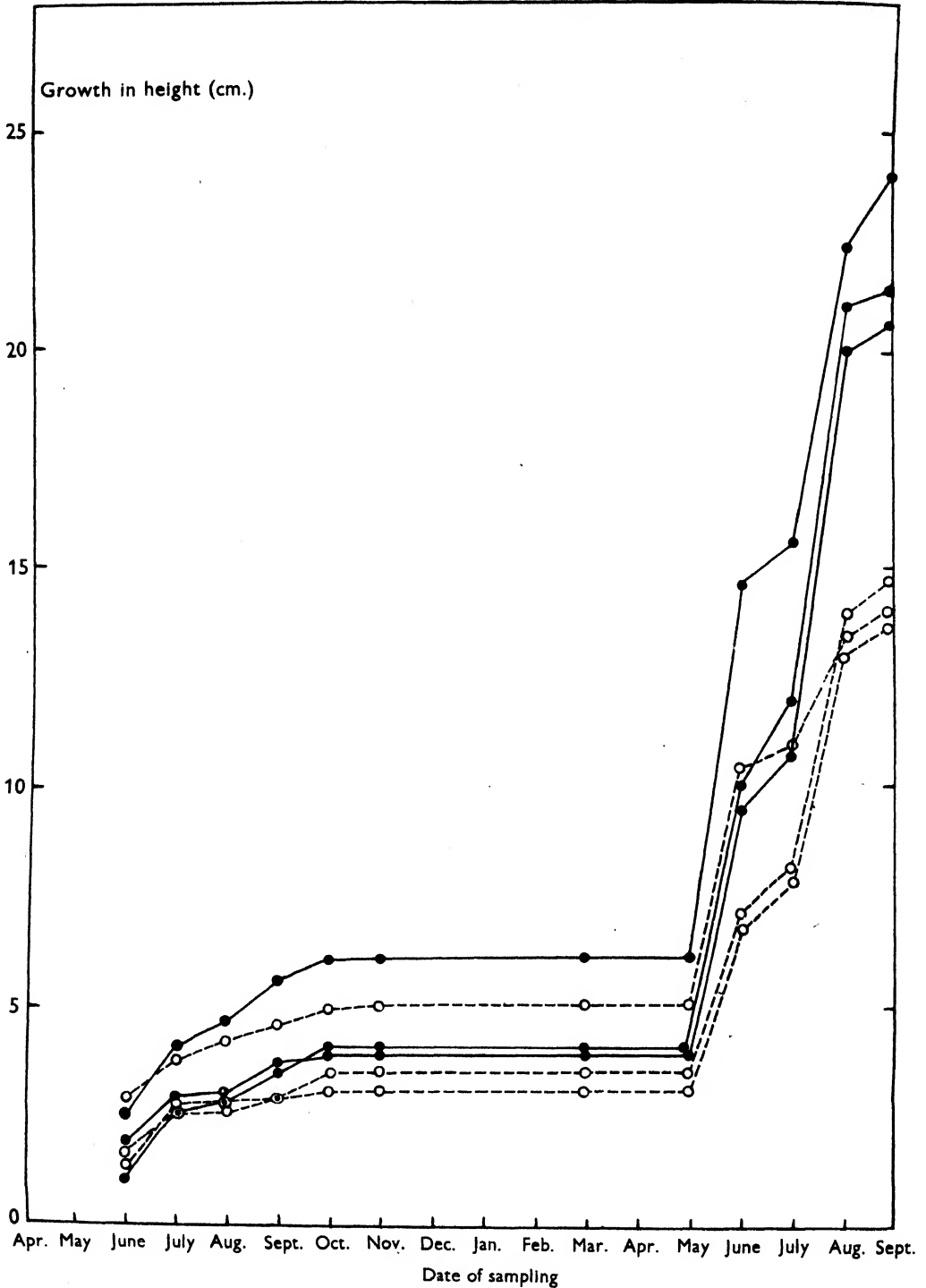


Fig. 1. Height growth of batches of beech seedlings grown through two seasons. In this and succeeding figures solid circles and full lines —●—●— refer to calcareous soils, whilst clear circles and broken lines —○—○— refer to non-calcareous soils.

thereafter the rate of growth decreased so that at the end of the experiment the three non-calcareous soils had produced seedlings of similar height.

Subjective estimates of vigour obtained by several methods of scoring by independent observers confirmed that the performance of seedlings on soil no. 4 differed throughout the first growing season from those on the other non-calcareous soils. The most likely cause of these differences is to be found in the date of coming into leaf. In each year the seedlings on soil no. 4 came into leaf earlier than any others and were, in each case, between a week and a month earlier than those on the other non-calcareous soils; whereas they preceded those of the calcareous soils by only one to four days.

(These results were obtained by recording the date on which, for the first time, some buds on 95% of the plants of any given treatment had come into leaf.)

Table 3. *Measurements of seedlings*

Type of soil	(Length in cm. Areas in sq.cm. Weights in g.)					
	...	Calcareous soil			Non-calcareous soil	
Serial no.	1	2	3	4	5	6
Height increment	24.1 \pm 0.81	21.4 \pm 1.15	20.4 \pm 0.47	13.2 \pm 0.88	14.7 \pm 1.11	14.0 \pm 1.71
Total dry weight	26.33	21.63	19.04	16.41	16.81	14.93
Dry weight excluding leaves	22.26 \pm 1.34	17.94 \pm 1.33	15.60 \pm 0.87	14.10 \pm 0.82	14.42 \pm 0.98	12.71 \pm 1.13
Dry weight of shoots excluding leaves	8.58 \pm 0.47	6.98 \pm 0.49	6.66 \pm 0.48	4.96 \pm 0.27	4.70 \pm 0.29	4.68 \pm 0.39
Dry weight of stem	5.32 \pm 0.29	4.42 \pm 0.31	4.48 \pm 0.23	3.53 \pm 0.22	3.42 \pm 0.22	3.47 \pm 0.30
Dry weight of branches	3.26 \pm 0.24	2.56 \pm 0.20	2.18 \pm 0.16	1.43 \pm 0.12	1.28 \pm 0.09	1.21 \pm 0.15
Dry weight of roots	13.68 \pm 0.96	10.96 \pm 0.89	8.94 \pm 0.56	9.14 \pm 0.59	9.72 \pm 0.66	8.03 \pm 0.78
Dry weight of tap root	8.28 \pm 0.56	6.57 \pm 0.34	5.87 \pm 0.31	4.99 \pm 0.32	4.99 \pm 0.32	4.29 \pm 0.41
Dry weight of root branches	5.40 \pm 0.52	4.39 \pm 0.45	3.07 \pm 0.31	4.15 \pm 0.33	4.73 \pm 0.39	3.74 \pm 0.33
Number of leaves	72.9 \pm 4.26	63.2 \pm 4.13	60.0 \pm 3.76	47.2 \pm 2.83	47.3 \pm 2.70	44.3 \pm 3.76
Dry weight of leaves per plant	4.07 \pm 0.21	3.69 \pm 0.20	3.44 \pm 0.18	2.31 \pm 0.14	2.39 \pm 0.13	2.22 \pm 0.21
Dry weight of leaves \times 10	0.56	0.58	0.57	0.49	0.51	0.50
Area of leaf	12.7	12.3	12.3	10.0	10.3	10.7
Area of leaf crop per plant	9236	7742	7350	4720	4886	4727

The results of some of the final measurements are given in Table 3 which shows that there is a greater contrast between seedlings of calcareous and non-calcareous soils than between those from individual soils of each type. The seedlings on the calcareous soils differed from those on the non-calcareous soils in a great variety of ways, for instance, they significantly exceeded them ($p > 0.05$) in the following respects: height, total dry weight, dry weight of complete stems, dry weight of main stem and of branches, dry weight of tap root, number of leaves per plant, dry weight of leaves per plant. Hence the growth rate

on these calcareous soils exceeds the growth rate on these non-calcareous soils under the stated experimental conditions. The differences in structure and texture between the soil of each group were such as to lead to the supposition that the differences were the result of other factors common to each group.

Within the group of calcareous soils there was somewhat greater variation in a number of characteristics than within the non-calcareous group. Indeed, the soil no. 1 produced seedlings which exceeded those of all the other soils in the following respects ($p > 0.05$): height, total dry weight, dry weight of the main stem and of its branches, dry weight of the whole root system and tap root, and number of leaves. It is notable that this soil appeared to possess the greatest activity of soil processes of any of the soils, as judged by such features as carbon-nitrogen ratio and nitrate-forming capacity. The Morgan soil test, too, suggested that it contained the highest available potassium content. These results suggest that under experimental conditions the rate of growth of young beech is greatest in calcareous soils, especially those containing a high concentration of available bases.

THE EFFECT OF SOIL CONDITIONS ON THE FORM OF THE PLANT

The striking differences already described between the plants on calcareous and non-calcareous soil do not express satisfactorily the difference in performance of beech on these soil types. There were very definite differences in form in addition to the differences of size. Differences of form may be studied by comparing the ratios of the means of any given pair of measurements, such as, for instance, the ratio of root-weight to shoot-weight. Since such ratios may vary in magnitude with size, and since the limits of variation in size as measured, for example, by weight, were different in each soil type, the comparison of such ratios cannot be simply made. The effects of soil condition upon form may, therefore, best be studied by comparison of groups of plants of equal size derived from each soil type. For such comparisons the criterion of size adopted here is the total dry weight of the permanent axis (stem + roots). The ratios under consideration have been calculated for groups of plants between certain limits of axis weight (0-5, 5-10, 10-15 g., etc.) and a graph has been constructed for comparison in each case. As might be expected, there is less difference in form between the treatments in the lower-size classes than in the higher-size classes. The smaller seedlings have departed less from their initial state.

THE FORM OF THE SHOOT

During the growing period it was clearly discernible that the frequency of branching of the stem of the seedlings growing in calcareous soils was greater than that of the others. Fig. 2 shows the ratio of the dry weight of stem branches to the weight of the main stem, plotted against total axis weight calculated by the method outlined above. It can be seen that plants of equivalent weight on calcareous soil and non-calcareous soil produce different relative weights of branches, except in the lowest size classes. The calcareous soils produce seedlings with more highly ramified stems.

The comparison of the whole population from calcareous and non-calcareous soils indicates that those from the former bear larger numbers and greater weights of leaves. Fig. 3A, B indicate that these criteria of leafiness increase, as would be expected, with the total weight of the axis, and there seems evidence from Fig. 3A that the leaf weight of plants on calcareous soil is greater than that of non-calcareous soils, irrespective of plant size. Fig. 3B, showing number of leaves, does not give quite so clear an indication of

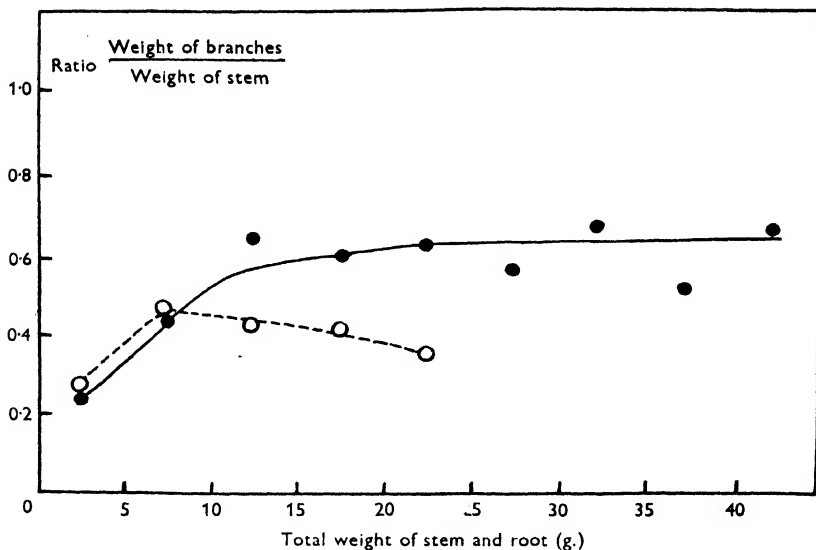


Fig. 2. Ratio of dry weight of stem branches to weight of main stem, plotted against total weight of the permanent plant axis.

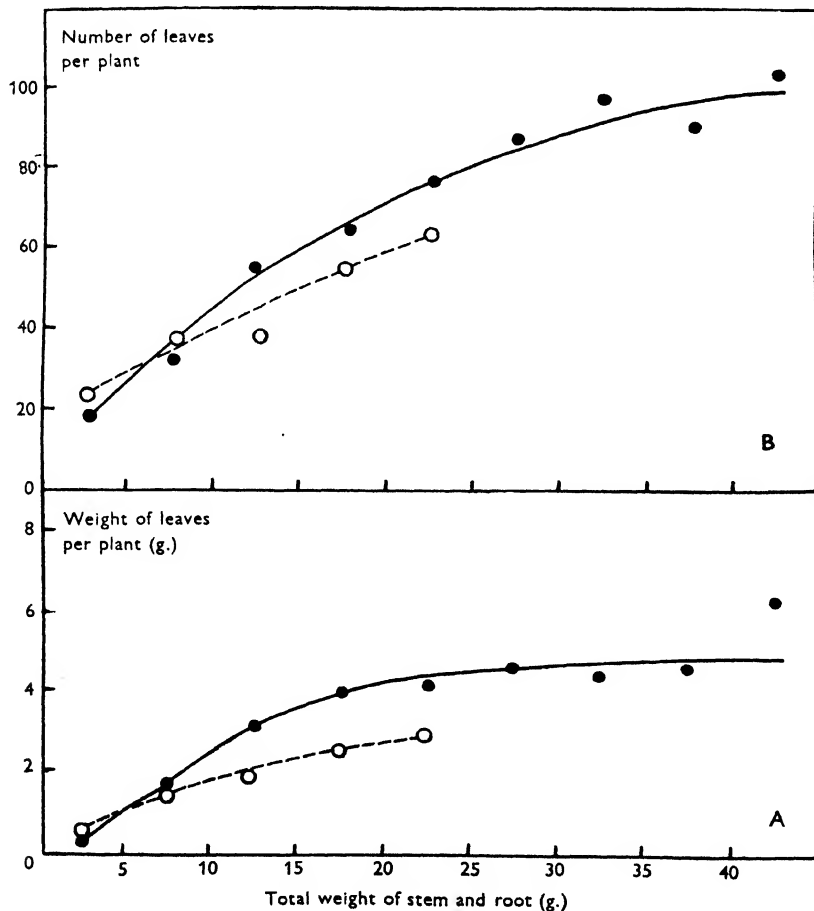


Fig. 3. A, weight of leaves per plant; and B, number of leaves per plant plotted against total weight of the permanent plant axis.

greater leafiness on the calcareous soils. The figures for area cannot be used for such a comparison since they are based on pooled random samples from the leaves of each plant.

RELATIVE ROOT AND SHOOT GROWTH

The relative root and shoot growth on the soils of the two types may be expressed in the form of root/shoot or root/stem ratio. Using root/stem ratio, the following mean figures were obtained in terms of dry weight:

Soil no. ...	Calcareous soil			Non-calcareous soil		
	1	2	3	4	5	6
Root/stem	1.59	1.57	1.34	1.84	2.07	1.72

Taken on this basis the root/stem ratio is significantly greater on the non-calcareous soils. Fig. 4 A shows the root/stem ratio plotted against the dry weight of the permanent axis and

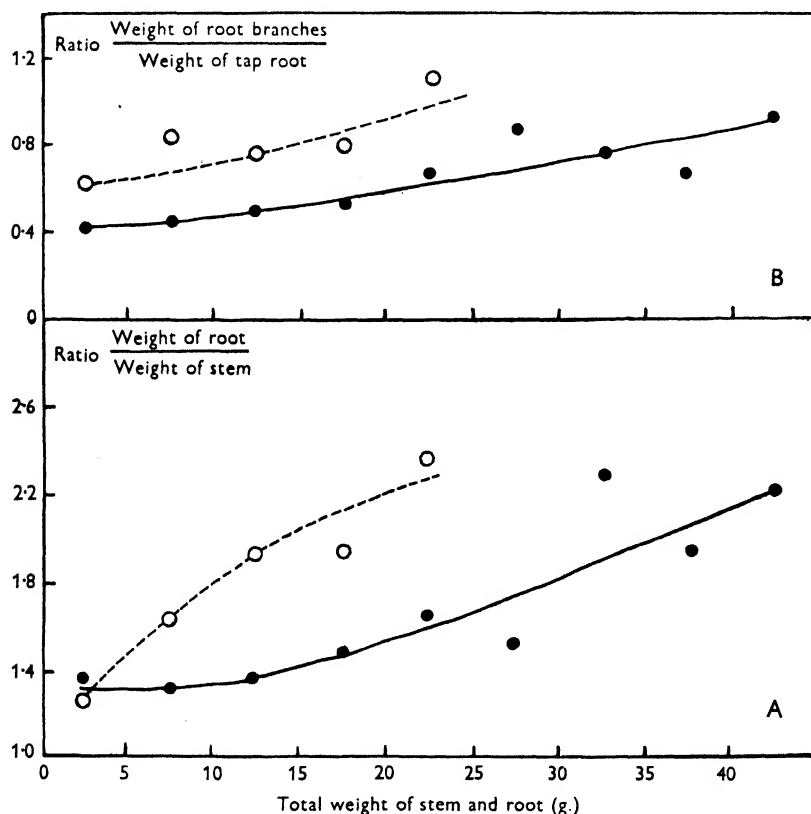


Fig. 4. A, the proportional weight of root to stem plotted against total dry weight of the permanent axis of the plant; B, the proportional weight of lateral roots to main tap roots, plotted against total dry weight of the permanent axis of the plant.

there is a trend of increase of the ratio with total axis weight. This trend is steeper on non-calcareous soil. It is clear, therefore, that the figures quoted above, derived from the means of the whole population on each soil type, minimize the differences in root/stem ratio because the larger seedlings from the calcareous soils are included in the comparison. Hence, it is reasonable to conclude that there is a proportionately greater root develop-

ment on non-calcareous soils due to the influence of soil factors and irrespective of the total growth made.

Figures for the proportional weight of lateral roots to main tap roots are plotted in similar fashion on Fig. 4 B. It is clear from this that the relatively greater weight of roots as compared with shoots on non-calcareous soil is associated with the greater development of laterals. This feature was exceedingly obvious when the plants were harvested and it was recorded that there appeared to be a lesser tendency to lignification of the laterals on non-calcareous soil. The greater development of roots on these soils seems, therefore, to be due in great part to the increased number of fine, unthickened lateral roots.

THE FORM OF THE LATERAL ROOT SYSTEM

The root systems of each plant were inspected when harvested, and a sample of the laterals of each was detached and preserved. The following notes on the whole root systems were made:

(1) On non-calcareous soils the seedlings produced a very much more extensive lateral root system. The main laterals were long and bore a great number of long and short branches.

(2) The lateral root systems of plants of calcareous soils consisted of fewer and shorter main laterals, less frequently branched.

(3) Some mycorrhizal infection was present on all seedlings and, judging from a rough enumeration, short lateral infected systems were most abundant on the two non-calcareous soils from Beech Woodland, nos. 4 and 5, and least from the third non-calcareous soil, from the Bagshot Sand, no. 6.

(4) The colour and appearance of the roots from the last-named soil, no. 6, differed from those of the others. They were dark brown or grey and showed a clear preponderance of long sublaterals over short sublaterals. The roots of the remaining soil types were light brown and those from soil no. 3 were the least branched and most compact of any, and showed the greatest degree of lignification, as judged by rigidity.

The samples of laterals which had been preserved were mounted in glycerine jelly and examined with lens or with a microscope to obtain confirmation of these descriptions. Long sublaterals were present on all the samples examined but were most prevalent on soil no. 6, and least on soil no. 5. On these long sublaterals root hairs were developed in every case and consequently root-hair development was recorded as most abundant on the roots of plants from soil no. 6.

A rough assessment of fungal colonization of the root systems was obtained as follows by estimating:

(a) The percentage of laterals bearing obvious mycorrhizal systems of monopodially branched short branches, visible to the naked eye.

(b) Percentage of laterals having smaller or simpler monopodial systems, visible with a lens.

(c) The percentage of laterals, relatively simple in form, which required microscopical examination to confirm the absence of root hairs and the presence of a fungal sheath.

The results are given in Table 4.

Table 4. *Rough enumeration of mycorrhizal infection*

Soil no.	Percentage of laterals bearing bunched systems (a)	Percentage of laterals clearly infected (b)	Percentage of laterals needing microscopical con- firmation (c)	Percentage of laterals uninfected (d)
1	29	23	48	—
2	32	39	29	—
3	30	42	28	—
4	34	39	27	—
5	48	27	25	—
6	17	25	58	—

The production of long sublateral systems was examined by recording the percentage of laterals bearing a majority of such branches; the results were:

Soils ...	1	2	3	4	5	6
	27 %	32 %	24 %	33 %	20 %	65 %

These semi-subjective estimates of root form and fungal infection do not show a very great spread in numerical results, but the following conclusions may reasonably be drawn:

(1) That the soil from the Bagshot Sand, no. 6, produced seedlings having fewer mycorrhizal rootlets and a higher percentage of long sublateral roots with root hairs than any other soil.

(2) The soil from the Beech Wood, no. 5, produced seedlings with the highest percentage of well-developed mycorrhizal systems and the fewest long sublaterals of any of the soils.

(3) The Garden soil, no. 1, produced seedlings whose root systems needed, in about half the cases observed, microscopic observation to determine the presence of mycorrhizal infection, for certain.

(4) The remaining soils were relatively similar by the method of enumeration used, except that soil no. 3, from Calcareous Beech Wood, produced fewer long sublaterals than nos. 2 and 4.

Hence there seems to be no correlation between mycorrhizal infection estimated in this way and the differences in size and form observed between the seedlings from calcareous and non-calcareous soils.

It seems likely, therefore, that the differences in size and form recorded may arise more directly out of soil conditions than by any effect of mycorrhiza.

DISCUSSION

The soil series here studied, though divisible into two well-defined groups of calcareous and non-calcareous soils, is deficient in examples of non-calcareous soils containing a high concentration of available nutrients. When the experiment was originally designed, these six soils were chosen for particular reasons. But since the experiment as originally designed was not completed, it is felt that these results, as far as they go, are worth putting on record. The points which may be made are:

(1) The growth of seedlings was greater in respect of size and weight upon the calcareous soils.

(2) There was a contrast in form between the seedlings from the two soil types, for the calcareous soils produced seedlings with greater development of the stem and its branches and a greater leafiness. The non-calcareous soils produced seedlings with a greater development of roots and their branches.

(3) By the method of determination here used, the mycorrhizal infection does not follow closely either the soil type or the seedling size.

Lindquist (1931) found a direct relation between decrease in acidity and increase in number of beech seedlings in natural forests in Sweden; and he believed this to be discernible in British beechwoods, too. The evidence from this present experiment is that the vigour of growth in neutral to alkaline calcareous soils is greater than that in non-calcareous soils, so that the phenomena observed by Lindquist may be due to a direct effect of soil factors rather than through the effects of associated or competing organisms.

The increased relative root growth on acid soils conforms with previous work on forest seedlings (for example, Aldrich-Blake, 1932; Burger, 1930; Mitchell, 1939) where it has been indicated that on soils poor in nutrients relative root growth is greatest.

The work of Hatch (1936-7) and of Finn (1942) shows that on any one soil mycorrhizal seedlings may develop a smaller relative root growth than uninfected seedlings, when infection is associated with increased absorption of minerals. Such variations as have been observed here are not associated with such great changes of root/shoot ratio as to overcome the tendency to develop extensive roots on acid soil and less extensive roots on the more nutritious calcareous soil. The drawing of further conclusions seems inadvisable since the detail of the structure of the mycorrhizas could not be examined in the present experiment.

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THE VEGETATION OF MAGNESIAN LIMESTONE CLIFFS AT MARKLAND GRIPS NEAR SHEFFIELD

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(With Plate 1 and ten Figures in the Text)

Outstanding characteristics of the Magnesian Limestone outcrop to the east of Sheffield are the 'grips', deep valleys with vertical cliff-like sides, believed by geologists to have arisen by collapse of the roofs of subterranean stream-channels. At Markland Grips, about 12 miles south-east of Sheffield near Clowne (Derbyshire) there are two such valleys joining just below that length of the right-hand valley which was chosen for detailed study (Fig. 1). Attention was focused chiefly on the vegetation of the cliff and of the scree at its foot. The plateau between the two valleys was planted or semi-natural woodland before it was felled during the war of 1914-18, since when most of it has been left to regenerate naturally. It is now covered with secondary woodland of *Betula* and *Fraxinus* with some *Acer pseudo-platanus*, *Ulmus glabra*, *Quercus robur*, *Taxus baccata*, *Sorbus aucuparia* and *Ilex aquifolium*, and with locally dense scrub and undergrowth of *Cornus sanguinea*, *Crataegus monogyna*, *Ligustrum vulgare*, *Rubus fruticosus* and *Rosa* spp. The oldest trees are between 20 and 30 ft. in height and there are numerous young plants of *Fraxinus*, *Betula*, *Sorbus aucuparia* and *Quercus*. No detailed examination was made of the vegetation of the plateau, but many calcicolous herbs, including *Viola hirta*, *Poterium sanguisorba* and *Origanum vulgare* were noticed along the sides of the marginal ride.

The cliff top. Between the marginal ride and the edge of the cliff is a narrow strip whose vegetation appears to be more natural than that of the plateau. The dominance of ash and birch is here less complete, while oak, elm and yew are more abundant and the trees have attained greater dimensions than on the plateau (Table 5), birches being found up to 49 ft. high with girths at breast height up to 42 in. Occasional trees of *Tilia platyphyllos* are found. Tree regeneration is proceeding actively and it is interesting that saplings of *Fraxinus* are more abundant than those of *Betula*, reversing the order of abundance of the larger trees (Tables 2 and 3). It seems likely that *Fraxinus* may ultimately replace *Betula* as the community approaches maturity.

Table 1. *Composition of vegetation of cliff top*

Trees	<i>Betula</i> spp.	l.d.	<i>Taxus baccata</i>	l.d.
	<i>Quercus robur</i>	f.	<i>Ulmus glabra</i>	f.
	<i>Fraxinus excelsior</i>	f.	<i>Tilia platyphyllos</i>	o.
	<i>Sorbus aucuparia</i>	o.		
Shrubs	<i>Corylus avellana</i>	d.	<i>Ligustrum vulgare</i>	l.a.
	<i>Cornus sanguinea</i>	l.a.	<i>Crataegus monogyna</i>	f.
	<i>Viburnum opulus</i>	f.	<i>Sambucus nigra</i>	o.-l.f.
	<i>Rhamnus frangula</i>	r.		
Field layer under shrubs	<i>Mercurialis perennis</i>	l.d.	<i>Hedera helix</i>	l.d.
	<i>Sanicula europaea</i>	l.f.	<i>Brachypodium sylvaticum</i>	l.f.
	<i>Rubus fruticosus</i>	o.	<i>Viola riviniana</i>	o.
Field layer in openings	<i>Brachypodium sylvaticum</i>	f.	<i>Carex flacca</i>	f.
	<i>Scabiosa columbaria</i>	o.	<i>Centaurea nigra</i>	o.
	<i>Poterium sanguisorba</i>	o.	<i>Serratula tinctoria</i>	l.
	<i>Carex montana</i>	l.	<i>Avena pubescens</i>	l.

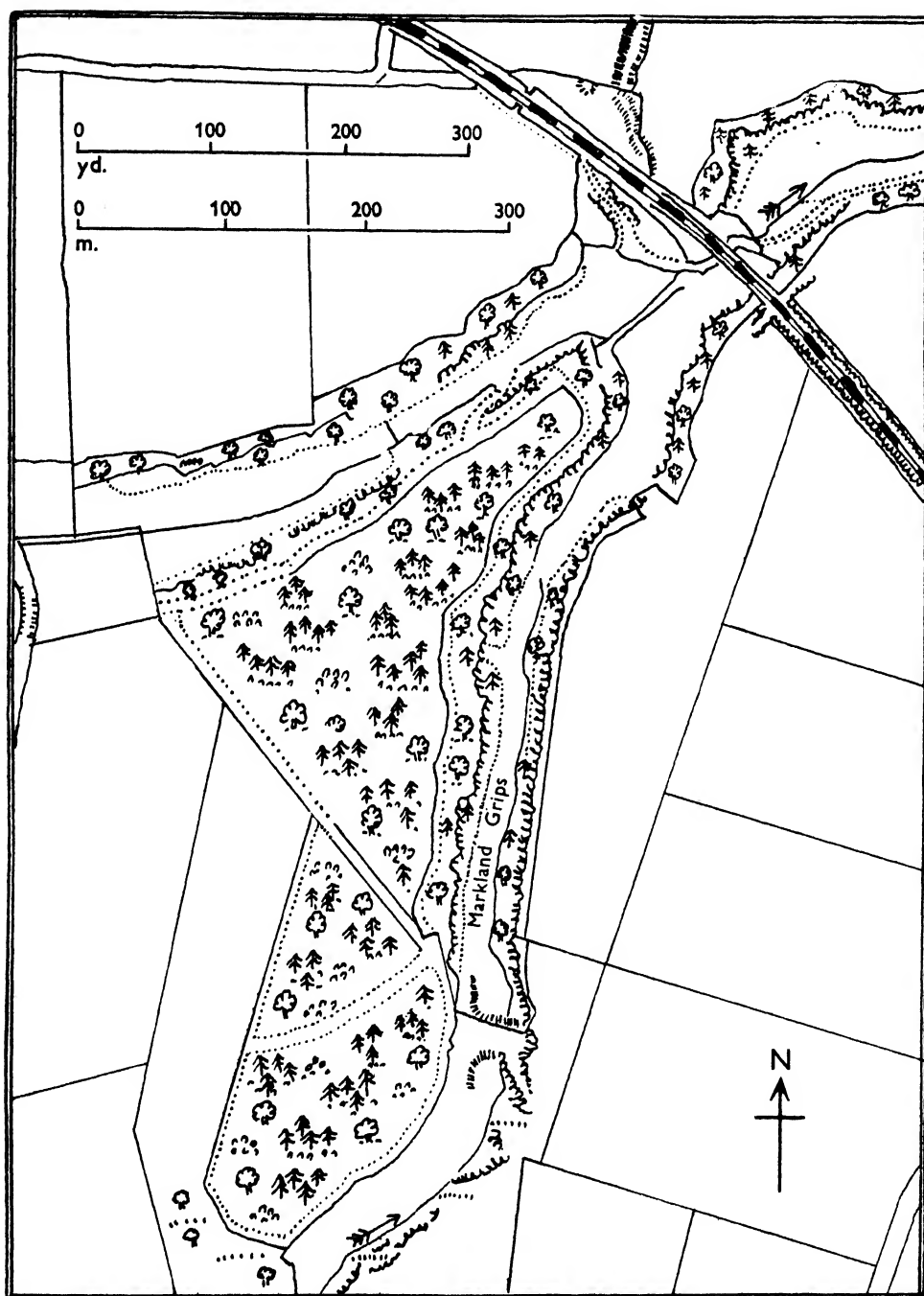


Fig. 1. Map of Markland Grips, reproduced from the 1916 edition of the Ordnance Survey map, with the sanction of the Controller of H.M.S.O. Scale 12·67 in. to 1 mile.

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Of particular interest is the abundance of *Taxus*, both of old trees and of seedlings of various ages. Its abundance increases towards the cliff edge and it becomes locally dominant just behind the edge.

Table 2. *Relative abundance of tree species in various habitats at Markland Grips*

Order of abundance	Plateau	Cliff top	Cliff edge	Cliff face	Scree
1	<i>Betula</i> spp.	<i>Betula</i> spp.	<i>Taxus baccata</i>	<i>Taxus baccata</i>	<i>Ulmus glabra</i>
2	<i>Fraxinus excelsior</i>	<i>Taxus baccata</i>	<i>Fraxinus excelsior</i>	<i>Betula</i> spp.	<i>Fraxinus excelsior</i>
3	<i>Quercus robur</i>	<i>Quercus robur</i>	<i>Quercus robur</i>	<i>Quercus robur</i>	<i>Betula</i> spp.
4	<i>Sorbus aucuparia</i>	<i>Ulmus glabra</i>	<i>Betula</i> spp., <i>Tilia platyphyllos</i>	<i>Fraxinus excelsior</i>	<i>Tilia platyphyllos</i>
5	<i>Ulmus glabra</i> , <i>Taxus baccata</i>	<i>Fraxinus excelsior</i>	<i>Ulmus glabra</i>	<i>Tilia platyphyllos</i> , <i>Sorbus aucuparia</i>	—
6	—	<i>Tilia platyphyllos</i> , <i>Sorbus aucuparia</i>	—	—	—

Table 3. *Relative abundance of tree seedlings and saplings*

Order of abundance	Plateau	Cliff top	Cliff edge	Cliff face	Scree
1	<i>Fraxinus excelsior</i>	<i>Fraxinus excelsior</i>	<i>Ulmus glabra</i>	<i>Ulmus glabra</i>	<i>Fraxinus excelsior</i>
2	<i>Quercus robur</i> , <i>Betula</i> spp., <i>Sorbus aucuparia</i>	<i>Taxus baccata</i>	<i>Fraxinus excelsior</i>	<i>Fraxinus excelsior</i>	—
3	<i>Taxus baccata</i>	<i>Quercus robur</i>	<i>Taxus baccata</i> , <i>Quercus robur</i>	<i>Betula</i> spp.	—
4	—	<i>Betula</i> spp.	<i>Sorbus aucuparia</i>	<i>Sorbus aucuparia</i>	—
5	—	<i>Ulmus glabra</i>	—	<i>Taxus baccata</i>	—
6	—	<i>Sorbus aucuparia</i>	—	<i>Tilia platyphyllos</i>	—

Table 4. *Relative abundance of shrub species*

Order of abundance	Plateau	Cliff top	Cliff edge	Cliff face	Scree
1	<i>Cornus sanguinea</i>	<i>Corylus avellana</i>	<i>Corylus avellana</i>	<i>Sambucus nigra</i>	<i>Sambucus nigra</i> , <i>Corylus avellana</i>
2	<i>Crataegus monogyna</i>	<i>Cornus sanguinea</i>	<i>Sambucus nigra</i>	<i>Crataegus monogyna</i>	<i>Crataegus monogyna</i>
3	<i>Corylus avellana</i>	<i>Crataegus monogyna</i>	<i>Ilex aquifolium</i>	<i>Corylus avellana</i>	<i>Cornus sanguinea</i>
4	<i>Viburnum opulus</i>	<i>Viburnum opulus</i>	<i>Cornus sanguinea</i>	<i>Cornus sanguinea</i>	—
5	<i>Rhamnus catharticus</i>	<i>Rhamnus frangula</i> , <i>Sambucus nigra</i>	<i>Crataegus monogyna</i>	—	—
6	—	—	<i>Viburnum opulus</i>	—	—
7	—	—	<i>Rhamnus catharticus</i>	—	—

The shrub-layer is well developed except under *Taxus*. The most prominent species (see Table 4) are *Corylus*, which is the general dominant, *Ligustrum vulgare* and *Cornus sanguinea*, the two last forming locally dense thickets up to 12 ft. high. *Rhamnus frangula* is an interesting constituent of the shrub layer.

The dominants of the sparse and interrupted ground flora are *Mercurialis perennis* and *Hedera helix*.

The cliff edge. The cliff edge is very irregular in height and direction, apparently as the result of frequent falls of rock, evidence for which can readily be found by an examination of the scree at the foot of the cliff. Tree counts (Table 2) show that *Taxus* is the most abundant tree on the edge, with *Fraxinus*, *Quercus* and *Sorbus aucuparia* all prominent. *Tilia platyphyllos* and *Sorbus torminalis* also occur. There are good reasons for believing

(p. 44) that these woody plants, and particularly *Taxus*, play an important part in detaching rocks from the edge of the cliff, so causing recession of the cliff face.

The cliff face. The number of trees on the actual cliff face is small, presumably because of the difficulties of establishment. The commonest species is *Taxus*, but there are numerous plants of *Ulmus*, *Fraxinus* and *Sambucus*. These seldom attain any great size but appear to fall away at an early stage carrying with them small fragments of rock. Some of the plants of *Fraxinus* and *Ulmus*, and also some of *Betula*, appear to have slipped from the edge and to have come to rest on a ledge lower down where they have succeeded in re-establishing themselves.

Table 5. *Maximum heights and girths of trees*

Species		Plateau	Cliff top	Cliff edge	Scree
Betula spp.	Height (ft.)	34	49	22	76
	Girth (in.)	23	42	17	60
Fraxinus excelsior	Height (ft.)	29	40	39	80
	Girth (in.)	15	26	33	115
Ulmus glabra	Height (ft.)	29	15	15	78
	Girth (in.)	12	6	10	90
Quercus robur	Height (ft.)	25	25	40	61
	Girth (in.)	30	46	76	88
Tilia platyphyllos	Height (ft.)	—	—	52	71
	Girth (in.)	—	—	84	99
				(main pole)	
Taxus baccata	Height (ft.)	20	30	33	35
	Girth (in.)	27	42	36	20
Sorbus aucuparia	Height (ft.)	25	—	29	—
	Girth (in.)	20	—	24	—
Crataegus monogyna	Height (ft.)	20	40	10	45
	Girth (in.)	16	38	6	36

Table 6. *Composition of woody vegetation of the cliff edge*

Trees	Taxus baccata	d.	Fraxinus excelsior	a.
	Quercus robur	f.	Sorbus aucuparia	f.
	Betula spp.	o.	Tilia platyphyllos	o.
	Ulmus glabra	o.	Sorbus torminalis	r.
Shrubs	Corylus avellana	f.	Sambucus nigra	f.
	Ilex aquifolium	o.	Cornus sanguinea	o.
	Crataegus monogyna	o.	Viburnum opulus	o.
	Rhamnus catharticus	o.		

It is a point of interest that on the whole *Ulmus* saplings occur near the top of the cliff and *Sambucus* towards the base, while *Taxus*, chiefly rooted in vertical fissures, is found at all levels.

Although the cliff face is quite sparsely vegetated, the species list is a long one. *Hedera helix* covers the largest area, followed by *Rubus fruticosus*. *Lactuca muralis* is abundant. The numerous mosses, liverworts and lichens were not studied closely and are not included in the list in Table 7. Fig. 2 is a chart showing the higher plants growing on a length of cliff face.

The scree slope. At the base of the cliff there is a talus slope which is colonized by woody plants except locally where recent heavy falls of rock have cleared small areas. There are numerous prostrate trees along this basal slope, some dead but some still living (Pl. 1, phot. 4). They include many which have certainly fallen from the cliff edge or face, but some appear to have been overturned by falls of rock.

The trees of the scree slope are larger than those of the plateau and cliff as can be seen from Table 5, and from the transect diagrams (Figs. 3–10). The most abundant tree is

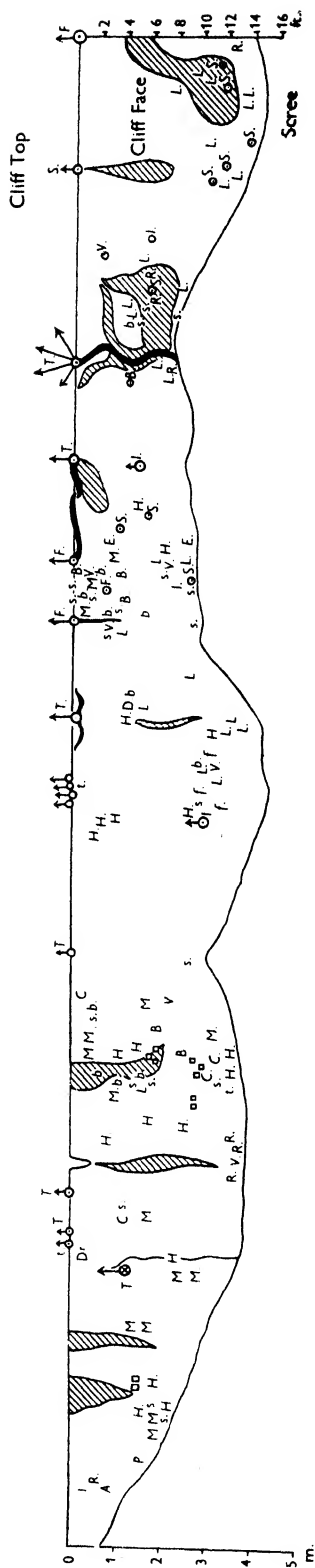


Fig. 2. Plants of the cliff face.

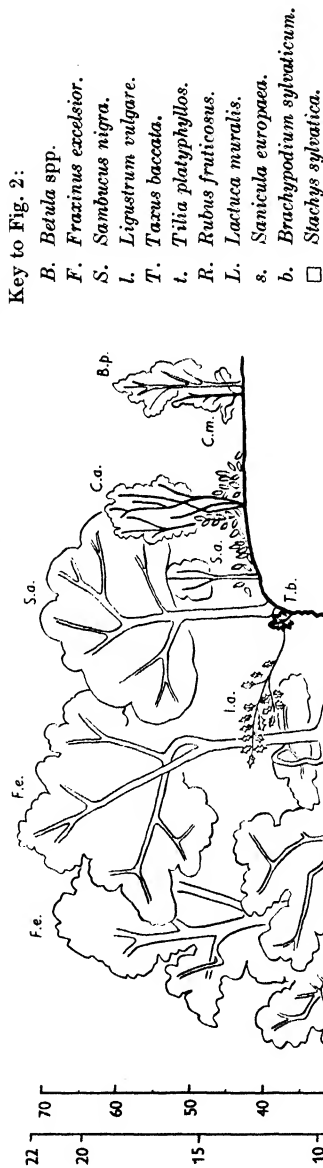


Fig. 3. Cliff profile showing falling *Fraxinus*, young *Taraxacum* cliff face, and well developed *Fraxinus* on scree.

Key to Fig. 2:

- Live tree
- ⊗ Dead tree.
- ▨ *Hedera helix*.
- ▩ *Hedera helix*.
- ▧ *Ilex aquifolium*.
- ▦ *M. Mercurialis perennis*.
- ▥ *E. Epilobium montanum*.
- ▤ *D. Dactylis glomerata*.
- ▣ *V. Viola* spp.
- ▢ *P. Primula veris*.

Key to legend of Figs. 3-9:

- F.e.* *Fraxinus excelsior*.
- C.m.* *Crataegus monogyna*.
- I.a.* *Ilex aquifolium*.
- C.a.* *Corylus avellana*.
- T.b.* *Taraxacum officinale*.
- S.n.* *Sambucus nigra*.
- B.p.* *Betula* spp.
- S.a.* *Sorbus aucuparia*.
- T.p.* *Tilia platyphyllos*.
- Q.r.* *Quercus robur*.
- U.g.* *Ulmus glabra*.

Ulmus glabra, after which come *Fraxinus*, *Betula* and *Tilia*. There are seedlings and young saplings of *Ulmus*, *Fraxinus* and *Betula*, but regeneration appears to have been limited in the past by cattle grazing, and no intermediate stages could be found between young saplings and large trees. Three seedlings of *Tilia platyphyllos* were found on the scree, but no later stages.

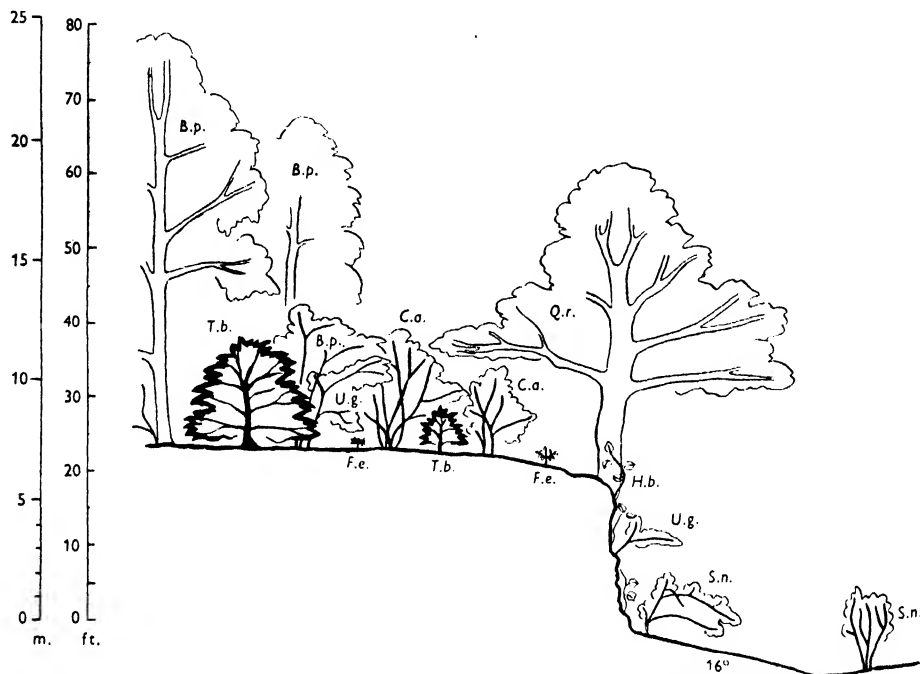


Fig. 4. Cliff profile showing young *Taxus* on cliff top, *Ulmus glabra* on cliff face, and tall *Betula* on cliff top.



Fig. 5. Cliff profile showing *Taxus baccata* on cliff edge, smaller cliff and steeper scree, well developed *Fraxinus* on scree.

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There is a well-developed shrub layer consisting mainly of *Sambucus nigra* and *Corylus avellana*. The prominence of the former suggests active nitrification, a view supported by the presence of *Mercurialis perennis*, *Urtica dioica*, *Galium aparine*, *Geranium robertianum* and *Melandrium dioicum*. The main dominant of the ground flora is *Mercurialis perennis* with *Scilla non-scripta*, *Sanicula europaea* and *Asperula odorata* locally abundant. *Viola riviniana* and *V. reichenbachiana* were both present, with some plants which could not certainly be assigned to either species and were presumed to be hybrids.

Table 7. *Composition of vegetation of cliff face*

Trees	<i>Taxus baccata</i>	f.	<i>Ulmus glabra</i>	o.-f.
	<i>Betula</i> spp.	o.	<i>Fraxinus excelsior</i>	o.
	<i>Quercus robur</i>	o.	<i>Tilia platyphyllos</i>	o.
	<i>Sorbus aucuparia</i>	o.		
Shrubs	<i>Sambucus nigra</i>	o.	<i>Crataegus monogyna</i>	o.
	<i>Ilex aquifolium</i>	o.	<i>Viburnum opulus</i>	o.
	<i>Corylus avellana</i>	o.	<i>Cornus sanguinea</i>	o.
	<i>Ligustrum vulgare</i>	o.	<i>Rosa</i> spp.	o.
Other angiosperms	<i>Hedera helix</i>	l.v.a.	<i>Rubus fruticosus</i>	l.a.
	<i>Lactuca muralis</i>	a.	<i>Sanicula europaea</i>	f.
	<i>Mercurialis perennis</i>	f.	<i>Brachypodium sylvaticum</i>	f.
	<i>Melica uniflora</i>	f.	<i>Geranium robertianum</i>	f.
	<i>Solanum dulcamara</i>	f.	<i>Viola riviniana</i>	f.
	<i>Urtica dioica</i>	f.	<i>Stachys sylvatica</i>	f.
	<i>Taraxacum officinale</i>	o.	<i>Epilobium montanum</i>	o.
	<i>Dactylis glomerata</i>	o.	<i>Solidago virgaurea</i>	o.
	<i>Fragaria vesca</i>	o.	<i>Senecio jacobaea</i>	o.
	<i>Hieracium</i> spp.	o.	<i>Campanula rotundifolia</i>	o.
	<i>Lonicera periclymenum</i>	o.	<i>Deschampsia caespitosa</i>	o.
	<i>Arctium vulgare</i>	r.	<i>Cirsium vulgare</i>	r.
	<i>Bromus ramosus</i>	r.	<i>Serratula tinctoria</i>	r.
	<i>Stellaria media</i>	r.	<i>Primula veris</i>	r.
Ferns	<i>Asplenium ruta-muraria</i>		<i>Cystopteris fragilis</i>	
	<i>Scolopendrium vulgare</i>		<i>Dryopteris filix-mas</i>	
	<i>Polystichum aculeatum</i>		<i>Dryopteris dilatata</i>	

Table 8. *Composition of the vegetation of the scree slope*

Trees	<i>Ulmus glabra</i>	l.d.	<i>Fraxinus excelsior</i>	f.
	<i>Betula</i> spp.	f.	<i>Tilia platyphyllos</i>	o.
	<i>Acer campestre</i>	o.	<i>Quercus robur</i>	o.
Shrubs	<i>Sambucus nigra</i>	a.	<i>Corylus avellana</i>	a.
	<i>Cornus sanguinea</i>	f.	<i>Crataegus monogyna</i>	f.
	<i>Prunus spinosa</i>	o.	<i>Ligustrum vulgare</i>	o.
Ground layer	<i>Mercurialis perennis</i>	d.	<i>Scilla non-scripta</i>	l.d.
	<i>Sanicula europaea</i>	l.d.	<i>Asperula odorata</i>	l.d.
	<i>Hedera helix</i>	f.	<i>Rubus fruticosus</i>	f.
	<i>Geranium robertianum</i>	f.	<i>Melandrium dioicum</i>	f.
	<i>Viola riviniana</i>	f.	<i>Viola reichenbachiana</i>	f.
	<i>Viola hirta</i>	f.	<i>Stachys sylvatica</i>	f.
	<i>Lamium galeobdolon</i>	f.	<i>Arum maculatum</i>	f.
	<i>Geum urbanum</i>		<i>Oxalis acetosella</i>	
	<i>Potentilla fragariastrum</i>		<i>Fragaria vesca</i>	
	<i>Veronica chamaedrys</i>		<i>Veronica montana</i>	
	<i>Glechoma hederacea</i>		<i>Anemone nemorosa</i>	
	<i>Orchis fuchsii</i>		<i>Arctium vulgare</i>	
	<i>Carex sylvatica</i>		<i>Dactylis glomerata</i>	
	<i>Brachypodium sylvaticum</i>		<i>Poa nemoralis</i>	

DISCUSSION

(a) *Role of woody plants in causing recession of the cliff face*

There is a good deal of evidence for the view that woody plants, and particularly *Taxus baccata*, play an active part in cliff recession. Their role is made easier by the chemical nature of the rock, its comparative softness and its numerous joints and bedding planes.

Our view is that *Taxus* seedlings establish themselves behind the cliff edge, extending their roots in all directions along existing cracks and bedding planes. The first obvious stage in the process of cliff breakdown is the appearance, usually some feet behind the present cliff edge, of a vertical fissure enclosing roots of *Taxus*. The fissure widens, pre-

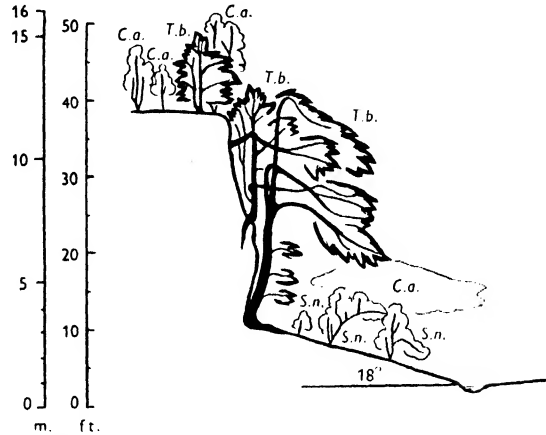


Fig. 6 Cliff profile showing *Taxus* in various positions on cliff edge and cliff face.

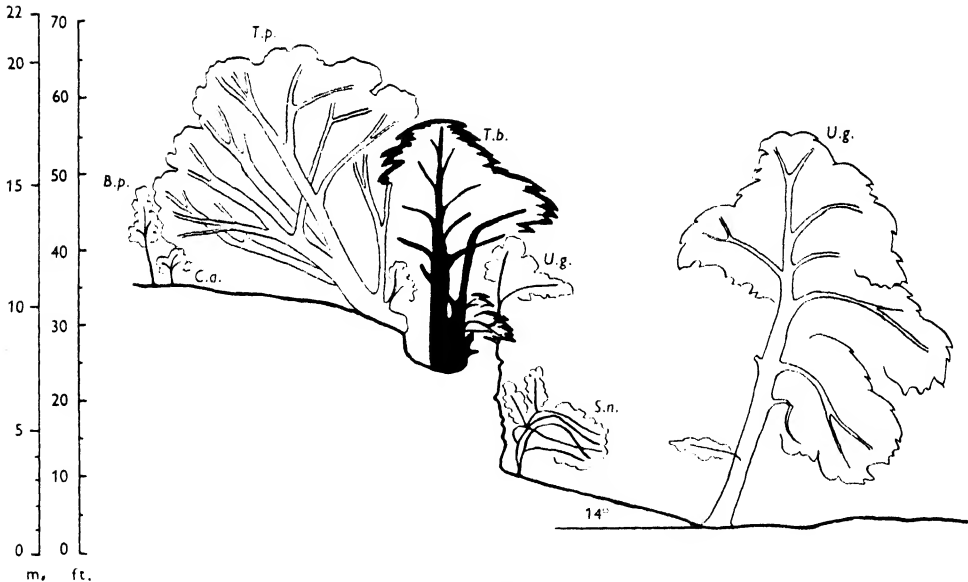


Fig. 7. Cliff profile showing *Taxus* in cleft, *Tilia* with many poles, and well developed *Ulmus glabra* on the scree.

sumably both by secondary thickening of the roots and by the action of drainage water, and debris accumulating at its bottom is commonly colonized by various nitrophilous species including *Mercurialis*, *Geranium robertianum* and *Urtica dioica*. Further enlargement ultimately brings about the detachment of a slab of rock which falls down to the scree-slope, leaving the root system exposed with its upper part in a funnel-shaped

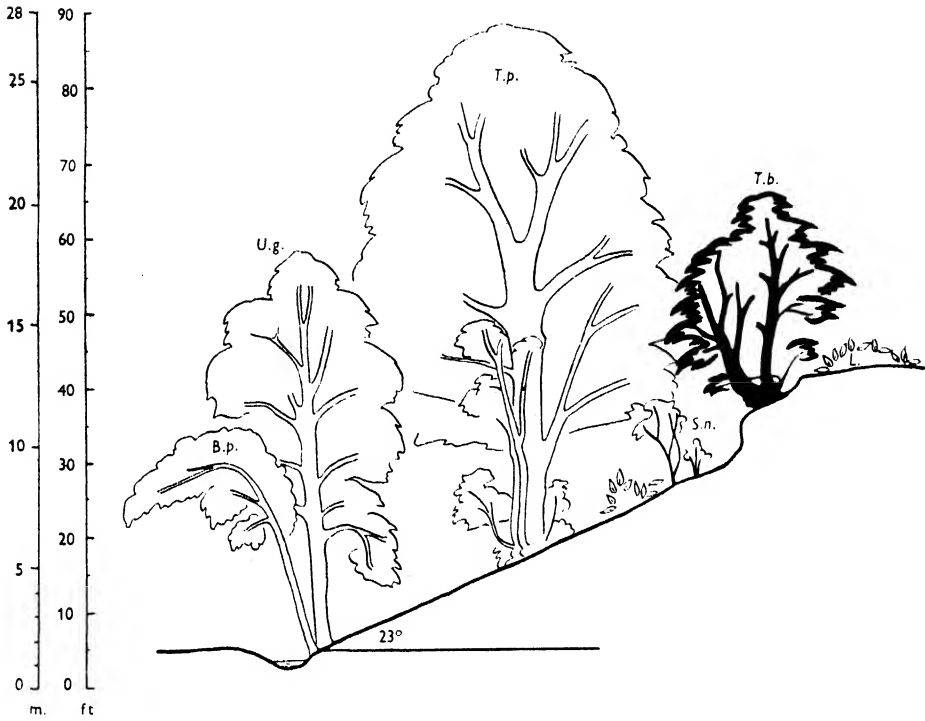


Fig. 8. Profile of a very small cliff and steep scree with a magnificent specimen of *Tilia* with one pole.



Fig. 9. Cliff profile showing *Tilia* on cliff edge with many poles, and *Tazus* on cliff face.

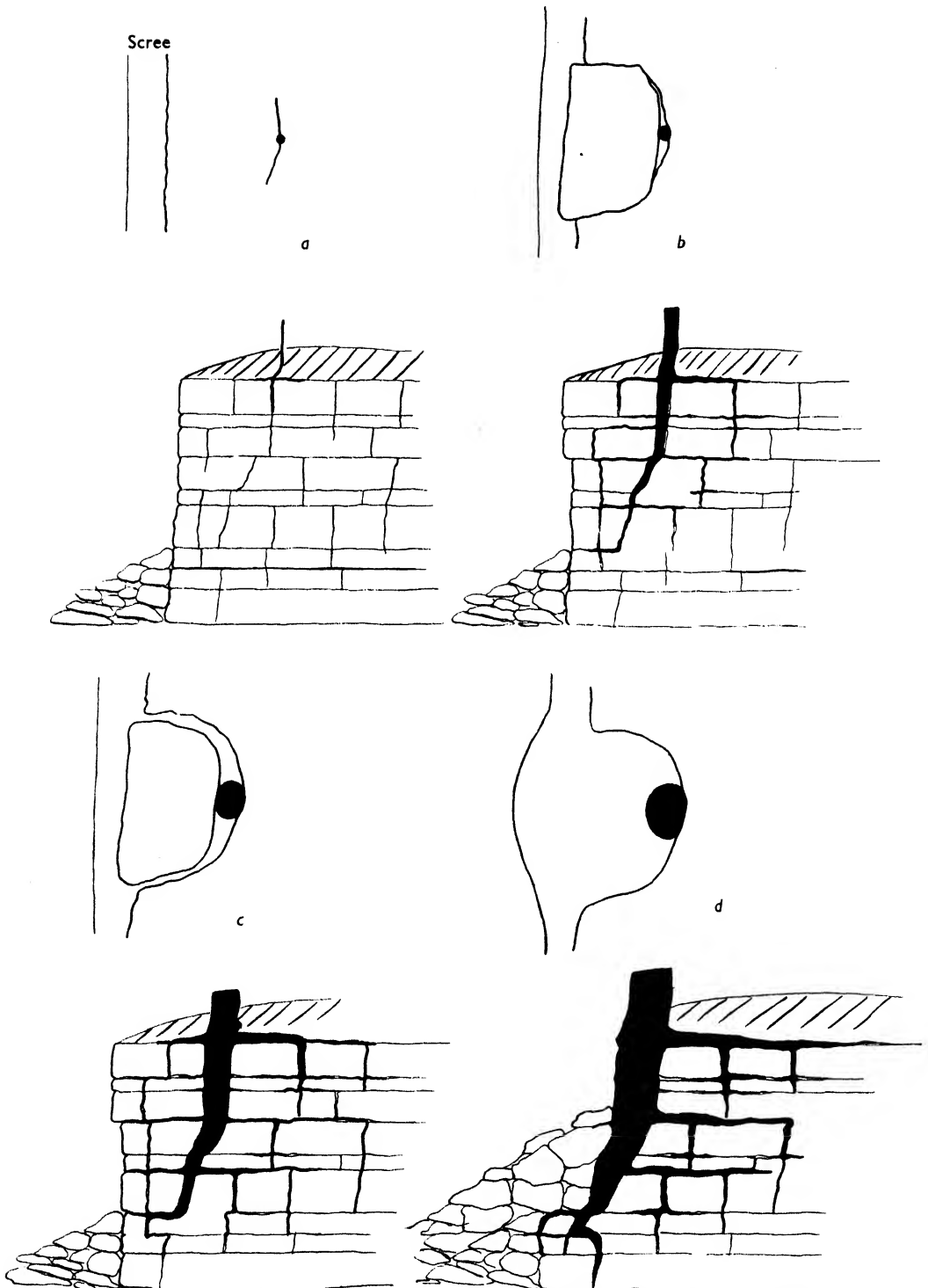


Fig. 10. Diagrammatic representation of stages of cliff breakdown (Plan and sectional views).

depression. A good example is shown in Pl. 1, phot. 3, where the fissure in which the tree was growing before the edge gave way must have been about 4 ft. across. Many of the yews are exposed in this way, and the disruptive effect of their extensive root systems may be judged from the fact that at a distance of 20 ft. from the base of the trunk roots may yet be more than 6 in. in diameter. In support of the view put forward are the facts that it is possible to find late stages of breakdown where the rock is still in process of being levered away from the cliff face (Pl. 1 and Fig. 10), and that in some of the exposed root systems there are tightly clasped rock fragments of various sizes whose presence can most easily be understood by supposing that the roots were formerly enclosed in rock behind the present face.

It is possible that *Taxus* sometimes establishes itself in a preformed fissure, and eventually completes the detachment of a rock slab in the way already described. Young yews have been found in such a position, but the great majority establish themselves well behind the cliff edge.

After detachment of the rock slab the exposed roots appear for a while to protect the new cliff face against further breakdown. This is most clearly seen where the roots have coalesced to form an extensive system closely appressed to the new face and reaching down into the basal debris and scree. The buttressing effect is also shown, though less frequently by *Tilia platyphyllos* and *Quercus robur*, but *Fraxinus*, *Betula* and *Ulmus glabra* often slip or fall when their roots are bared.

The preponderance of *Taxus* on the cliff edge is presumably the outcome not only of the successful establishment of its seedlings close to the edge but also of this temporary stabilizing effect of the exposed root system. Although other trees undoubtedly play some part in breakdown they seem soon to fall from the edge after their roots have been bared, and so form a smaller proportion of the trees to be seen on the edge at any time.

Any factors which shorten the life of *Taxus* will tend to hasten cliff recession. The most obvious of such factors at Markland Grips are *Hedera helix* and *Polyporus sulphureus*, one or both of which seem responsible for the several dead trees still standing on the cliff edge.

(b) *The status of Tilia platyphyllos at Markland Grips*

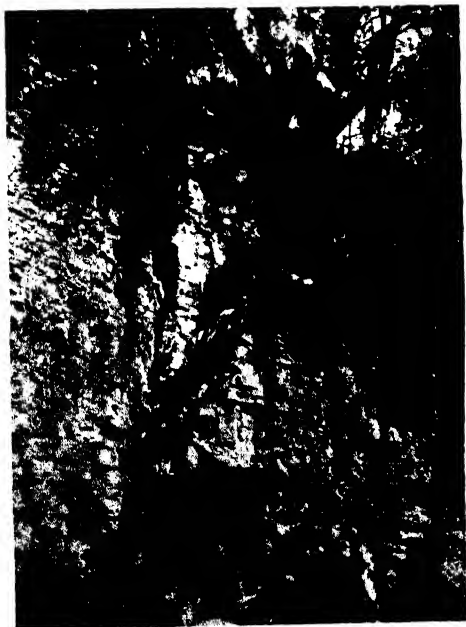
One of the most interesting features of the vegetation of the Magnesian Limestone to the east of Sheffield is the frequent occurrence both of *T. cordata* and *T. platyphyllos*. Both species are found on and near the cliffs at Anston Stones Wood (12 miles east of Sheffield), *T. cordata* is also nearby in Scratta Wood and has been recorded from Roche Abbey and from near Conisborough, while *T. platyphyllos* is at Markland Grips. *T. cordata* is undoubtedly native in Great Britain and there is no reason to doubt that it may persist as an indigenous tree even as far north as the Lake District. Its pollen grains are found in late Boreal and post-Boreal peats throughout England and Wales, reaching maximal frequency in Godwin's Zone VIIa (Godwin, 1940), though falling to very low values in Zone VIII, that is since the climatic deterioration in the Middle and Late Bronze Age. Only very locally in the south-west, close to the Wye Valley where it is still an abundant tree, does its pollen persist in appreciable quantity in recently formed peat. But elsewhere its occurrence as an occasional and local tree, especially on limestone slopes and cliffs, matches the sporadic appearance of its pollen in recent peats. It maintains itself by natural regeneration and is reasonably regarded as remaining a native tree.



Phot. 1. *Taxus* in a fissure.



Phot. 2. *Taxus* exposed where cliff face has broken away. Note collection of detritus at the base commonly colonized by nitratophilous plants.



Phot. 3. Cliff face completely broken away exposing *Taxus* root system. Note bedding planes and the shelf of rock at the base of the cliff.



Phot. 4. *Taxus* in a depression. Note fallen *Betula* lying across the scree.

T. platyphyllos is occasionally found growing with presumably native *T. cordata*, regenerating freely and occupying habitats on the edges or faces of cliffs where it certainly cannot have been planted. It has been judged native near Symonds Yat in the Wye Valley, in rocky mountain woods in south Wales (Hyde, 1931), in Shropshire, at Anston Stones Wood and Markland Grips near Sheffield, and farther north at Richmond in north-west Yorks (Sledge, 1944). At Markland Grips there are many fine trees, those on the scree slope usually being single-stemmed and reaching nearly 100 ft. in height (Table 5), those on the cliff edge commonly many-stemmed and less tall. Seedlings have been found and the tree appears to be maintaining itself by natural regeneration.

There are two important considerations which make it difficult to be certain that *T. platyphyllos* is in fact a native of Great Britain. In the first place, whereas *T. cordata* reaches nearly 64° N. in Scandinavia, Finland and Russia, *T. platyphyllos* is regarded as native only southwards of about 51° N. in continental Europe (Jaccard & Frey, 1928). In the second place, pollen of *T. platyphyllos* has never yet been found in British post-glacial peat. It can hardly have been overlooked since it is readily distinguishable from that of *T. cordata* (Godwin, 1940, p. 389). It is still possible that examination of peat-deposits close to the Magnesian Limestone outcrop may reveal its pollen. Meanwhile, it seems best to suspend judgement as to the status of *T. platyphyllos* in the British flora, remembering that lime timber was formerly prized for wood-carving and may well have been planted for this purpose in woods owned by the famous Cistercian abbeys which lay along this tract of limestone.

(c) Other species of floristic interest

Of further relevance to the problem of the status of *T. platyphyllos* at Markland Grips is the fact that the area is one of considerable floristic interest. Amongst woody plants mention should be made of *Sorbus torminalis*, young plants of which occur on the cliff edge and seem unlikely to have been derived from planted trees. Druce (1932) regards it as native as far north as Westmorland and Notts. *Rhamnus frangula*, which occurs in the strip along the cliff top, is commonly regarded as a shrub of acid soils (Druce, 1932), but is here in a strongly calcareous habitat.

The most interesting herbaceous plants of the area are perhaps the two Carices, *Carex montana* and *C. ericetorum*, both growing on grassy slopes over limestone higher up the valley, and *C. montana* also to be found by the marginal side which bounds the 'cliff top' strip of woodland. These are very local species in Great Britain, *C. ericetorum* being known only on the Breckland heaths between Newmarket and Thetford until it was discovered quite recently in a few localities farther north.

SUMMARY

1. An account is given of the ecology of the cliffs and scree-slopes at Markland Grips, a steep-sided valley in the Magnesian Limestone near Sheffield.

2. It is shown that woody plants, and especially *Taxus baccata*, play a significant part in causing cliff recession.

3. The status of *Tilia platyphyllos* is discussed, and it is concluded that there are strong reasons against regarding it as a native tree of the area.

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NOTES ON THE BURIED SEED POPULATIONS BENEATH DIFFERENT TYPES OF LEY IN THEIR SEEDING YEAR

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(With ten Figures in the Text)

Previous surveys of the buried viable seed content of soils have been made in relation to different types of vegetative cover or farming management. The viable seeds beneath grassland have been studied by Chippindale & Milton (1934), by Milton (1936, 1939) and by Champness & Morris (1948). Some workers have considered these populations in relation to the previous history of the areas (Milton, 1943, 1948; Brenchley, 1918; Oosting & Humphreys, 1940). They have shown the occurrence of viable seeds as representing an earlier phase in the succession through which the field has passed or is passing. Studies of the effects of cultural operations include experiments made at Rothamsted on the effect of fallowing (Brenchley & Warington, 1930, 1933, 1936, 1945) and investigations on pot scale by Chepil (1946). Attention has also been given to the difference between seed populations associated with grass and arable conditions and the effect of ploughing up (Brenchley, 1918; Prince & Hodgdon, 1946; Champness & Morris, 1948).

The present investigation is a 'pilot' experiment along a somewhat different line. In connexion with the extending use of special-purpose leys it was considered worth while to find whether or not different seeds mixtures affected the buried viable seed content of the soil. The first part of the investigation, the investigation of weed-seed populations at the end of the seeding year, is described here. Differences in the seeding year would seem to arise mainly from differences in the rates of establishment of the leys, although one mixture, that containing lucerne, was managed differently from the rest.

A prior consideration of the conditions involved and their probable effects suggested that the weed populations would be controlled by two factors acting antagonistically. It was therefore difficult to predict the results. First there is the possibility of differential germination of the seeds already in the soil. Levy (1940) suggests that light may be necessary for the germination of many weed seeds; both he and Donald (1941) offer this as a possible explanation of the long periods for which seeds, beneath a cover of vegetation, will remain viable in the soil without germinating. Differences in rate of establishment of ley are bound to produce differences in the amount of light reaching the soil surface. If it is true, therefore, that light is necessary for the germination of many weed seeds, there would be more germination and so fewer seeds left in the soil in the slowly establishing swards. The second factor is differential replenishment. In general this would be expected to increase with the quantity of weeds in the sward. The weediness of the sward would depend first on the number of seeds germinating and secondly on the opportunities for those seedlings to establish. Both would increase with slowness of establishment. The proportion of weed setting seeds would be controlled by grazing. If differential grazing should occur this would modify the relationship of weed-seed replenishment to rate of ley establishment. Opportunities to set seed in a grazed sward are more likely to occur with plants of low growth and rapid life cycle.

The balance of these two factors, differential germination and replenishment would then be expected to vary not only with the type of sward and its management but also with individual species according to their growth habit, their life cycle and the environment they require for germination. It would also be affected by the varying ability of seeds to lie dormant in the soil and to retain their viability over several seasons. The populations of microbiotic, or short-lived, species would of necessity be controlled by the replenishment factor alone, while replenishment might be insignificant compared with differential germination for macrobiotic species.

Before proceeding to outline the actual buried seed survey it is necessary to consider the seeds mixtures used. They were:

- (1) Perennial ryegrass S. 24 + white clover S. 184 + S. 100.
- (2) Perennial ryegrass S. 23 + white clover S. 184 + S. 100.
- (3) Cocksfoot S. 37 + white clover S. 184 + S. 100.
- (4) Timothy S. 48 + white clover S. 184 + S. 100.
- (5) Meadow fescue S. 53 + white clover S. 184 + S. 100.
- (6) *Bromus inermis* + white clover S. 184 + S. 100.
- (7) Lucerne Grimm, cocksfoot S. 37 + white clover S. 184 + S. 100.

All mixtures were sown on 1 April 1946. Mixtures 1-6 inclusive were unfenced and grazed on and off during the season. They represent a gradation in speed of establishment from the fastest, S. 24, successively to S. 23, S. 37, S. 53 and S. 48. *Bromus inermis* was very slow and the take exceedingly poor. The vegetation of these *Bromus* plots was largely composed of white clover and geranium (*Geranium dissectum* and *G. molle*). A rough analysis in the autumn showed that *Bromus* was contributing only 5% of the vegetation.

Both white clover and geraniums are low-growing plants. Since white clover is highly palatable these plots would be expected to be grazed low, and observations showed that this did, in fact, happen. Seed replenishment would then be low, despite the weedy nature of the sward, and would probably be confined to low-growing species. Selective grazing would have the reverse effect on the cocksfoot swards. There the tall growth and relative unpalatability of the grass would increase the proportion of weeds allowed to set seed.

Mixture 7, that containing lucerne, was fenced off and managed differently from the rest. It was allowed to grow unmolested until the autumn except for a light topping about midsummer. This management allowed ample opportunity for weeds to flower and set seed. The competition afforded by the tall growth suppressed short or prostrate weeds, but the taller weed species thrived.

METHOD

Two replicates of seven mixtures were sampled for buried seeds in November 1946. Two samples, one of the top 2½ in. and the second of the next 4 in. of soil were taken at each boring. The method used has been outlined in a previous paper (Champness & Morris, 1948). A total of fifteen borings was made on each plot. This number was chosen as it provided the convenient quantity of soil to fill the boxes available.

The soils were laid out over sand in wooden boxes and kept in the greenhouse. They were first watered at the beginning of March 1947, and were kept under conditions suitable for germination from then on for 19 months. Seedlings were removed and identified as soon as they were large enough. Tables of the number of seedlings germinating in each sample were constructed, and from those the weed-seed populations per acre were calculated.

RESULTS (1)

Total weed-seed populations

The average total population for each mixture is shown in Fig. 1. Outstanding is the high population beneath the lucerne mixture, and this confirms the observation that considerable seeding was allowed on these ungrazed plots. The difference between this lucerne mixture and the grazed plots is significant.

The viable seed content of the other swards shows a general increase from the more rapidly developing to the slower establishing swards, although the differences were not

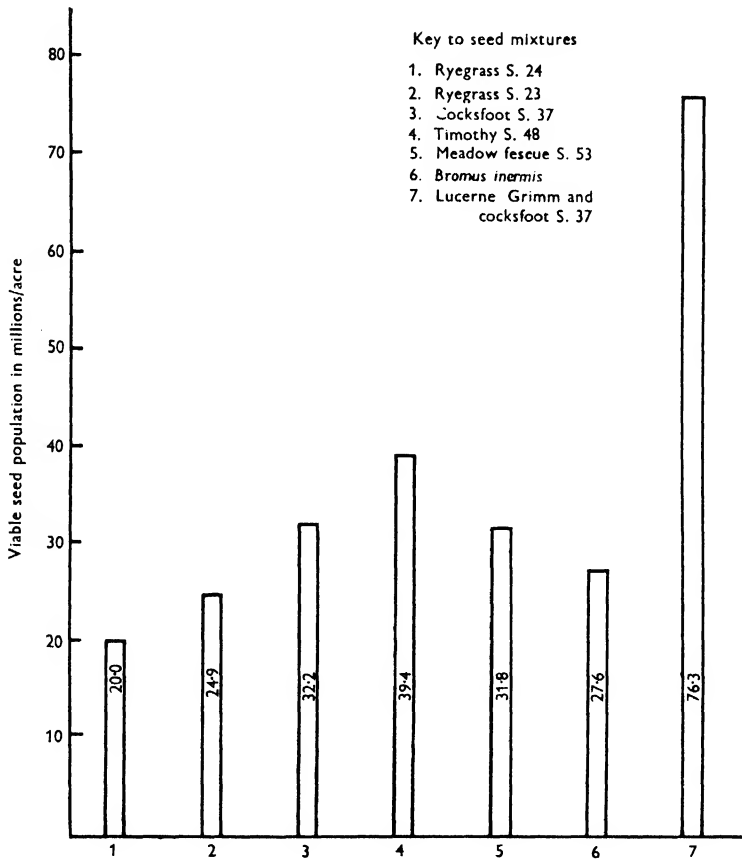


Fig. 1. Diagram showing total buried seed populations beneath different types of ley.

sufficient to be significant. The correlation between slowness of establishment and weed-seed population is, however, irregular. The viable seed population of the cocksfoot swards was greater, and the *Bromus* lower, than would be expected from their rates of establishment. The weed-seed populations thus show the same deviations from the order of rate of establishment as the deviations of the replenishment factor expected to result from differential grazing. It appears, therefore, that replenishment is the major factor controlling the weed-seed populations.

Key to seed mixtures

1. Ryegrass S. 24
2. Ryegrass S. 23
3. Cocksfoot S. 37
4. Timothy S. 48
5. Meadow fescue S. 53
6. *Bromus inermis*
7. Lucerne Grimm and cocksfoot S. 37

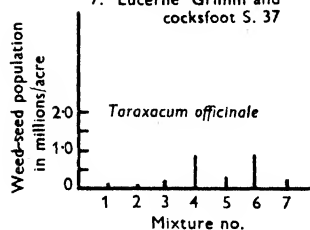


Fig. 2.

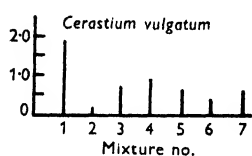


Fig. 3.

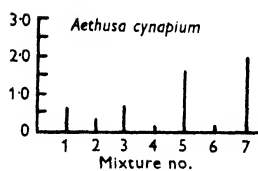


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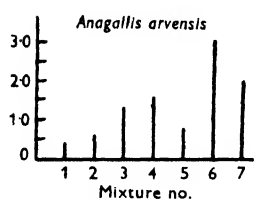


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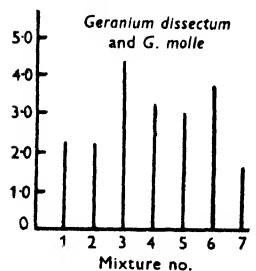


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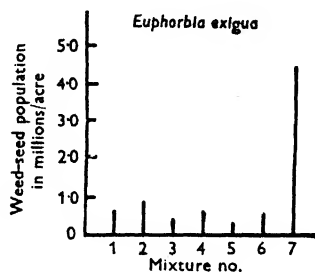


Fig. 7.

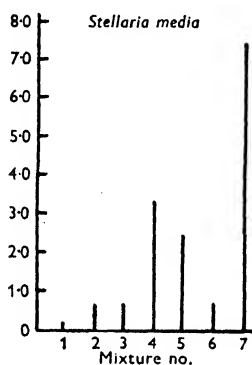


Fig. 8.

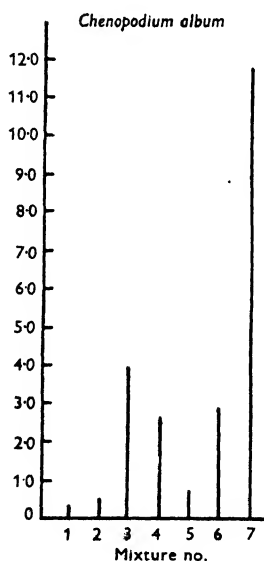


Fig. 9.

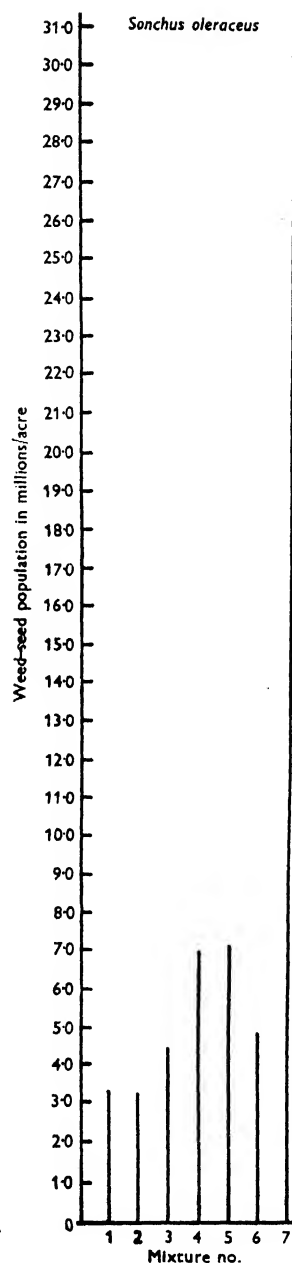


Fig. 10.

Figs. 2-10. Diagrams showing weed-seed populations of some individual species.

(2) *Populations of individual species*

Figs. 2-10 illustrate the viable seeds beneath each mixture of a range of species. They fall into three main groups: (a) Species with very high seed populations on the lucerne plots (Figs. 4, 7 and 10). These five species, *Aethusa cynapium*, *Euphorbia exigua*, *Stellaria media*, *Chenopodium album* and *Sonchus oleraceus*, all produced large quantities of seed when growing on the ungrazed lucerne plots. They are all plants of upright growth, although *Chenopodium* and *Sonchus* were the only two tall enough to enable their flowering heads to stand up above the lucerne and cocksfoot. The effect of the other seed mixtures on these five species varied. *Chenopodium* did well on the cocksfoot, presumably gaining from differential grazing. *Stellaria* succeeded on the non-aggressive timothy and fescue plots. Surprisingly little *Aethusa* was found on these latter plots. Viable seeds of *Sonchus* varied more or less in inverse proportion to the rate of establishment. (b) Species with high populations on all slowly establishing swards (Figs. 2, 5 and 6). *Anagallis arvensis*, *Geranium molle* and *G. dissectum* are all prostrate species and had high seed populations on all the slowly establishing swards, even the *Bromus inermis*, in spite of the close grazing. The geraniums also gave high populations on the cocksfoot plots, which in contrast were leniently grazed. *Taraxacum officinale* gave high populations on the timothy and *Bromus* plots. Replenishments here must be attributed more to the short interval between emergence of the flowering head and harvest, than to a low-growing habit. (c) Species showing no regular correlation between opportunities for replenishment and weed-seed populations (Fig. 3).

Cerastium vulgatum is included in the histograms as providing a good example of an instance where the population of viable seeds shows no regular relationship to opportunities either for germination or for replenishment. *Lolium perenne*, *Capsella bursa-pastoris*, *Ranunculus repens* and *Potentilla reptans* also show similar results. Generally they are species making only a minor contribution to the buried seed populations. Frequently they showed a high population on one plot, but not on both replicates. Presumably these occasional high figures are produced by a boring taken on a patch where a plant of the species concerned has grown and shed its seed. Such small centres of high population have been shown to occur (Champness, unpublished data).

Such patches of high population cause very irregular dispersion of the weed-seed populations. It is therefore desirable that a considerable number of borings should be taken from any plot investigated, and the fifteen borings used in this investigation cannot be considered as adequate to measure the differences in question.

DISCUSSION AND SUMMARY

The total weed-seed populations have been shown to parallel the expected opportunities for seed replenishment. In so far as these opportunities are related to the slowness of sward establishment the weed-seed populations increase with the lowering of the rate of establishment. Any effect of differential germination is completely masked by the replenishment factor.

The buried seed populations of certain species follow the same trend as the total buried seed populations, while others show considerable departures from it. In general, the taller species were able to replenish themselves best on the lucerne plots which were not grazed

until the autumn, while the lower growing species were most successful on the slowly establishing swards, and could not withstand the competition afforded by lucerne.

Given that replenishment is the major factor determining weed-seed populations under these conditions, differential germination might still be an important factor for species capable of surviving long periods in the soil without germination. *Anagallis* has been shown to remain viable in soil upwards of 10 years (Brenchley & Warington, 1936); the histogram for this species (Fig. 5) shows clearly, however, the dependence of its viable populations on replenishment.

The practical agricultural importance of this experiment will depend largely on the later stages of the investigation. If the differences in viable seed content of soils underlying different leys are perpetuated for several years, they may then influence retrogression and hence the productivity of the sward. If the land is ploughed such differences will affect the extent of weed competition to which the next crop is exposed. Observations made on certain trials conducted elsewhere show that differences in actual weediness of the sward which result from differences in rate of establishment may be perpetuated at least until the second harvest year (Williams, unpublished data). The plots were resampled in the autumns of 1947 and 1948, and it is hoped to resample in each autumn throughout the life of the leys. Thus it is hoped to find how far the differences initiated in the seeding year affect the weed-seed populations of succeeding years.

The author wishes to express her sincere thanks to Dr William Davies for granting facilities to carry out the investigation, and to thank Mr G. P. Hughes, Miss B. M. Baggs, Miss R. G. Collett and other colleagues for their ready help.

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THE GROWTH REQUIREMENTS OF *PORPHYRIDIVM CRUENTUM*: WITH REMARKS ON THE ECOLOGY OF BRACKISH WATER ALGAE

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(*With three Figures in the Text*)

I. INTRODUCTION

Porphyridium cruentum (Agardh) Naeg., a unicellular Rhodophycean, was first grown in pure culture by Kufferath (1912), who published a more detailed study in 1920 and reported again on his technique in 1930 (p. 179). By grinding the desiccated material and dispersing it in liquid agar, afterwards solidified in test-tubes, he obtained red colonies. The attainment of bacteria-free cultures is attributed by Kufferath to the use of various salts of organic acids employed in turn, so that eventually the contaminating organisms, only adapted to one or the other of them, were eliminated. The pure cultures were soon lost again owing to the difficulty of maintenance.

This success, so early in the history of pure cultures of algae, was not repeated until Vischer (1935) published his paper with a detailed and useful account of varied attempts to find a satisfactory medium, pure cultures having been obtained by transferring bits of material to moist filter-paper and allowing cells to creep out of the inoculum so that they could be inseminated on to agar plates. *Porphyridium* is the only red alga grown in pure culture.

In one respect Vischer's experience is in agreement with Kufferath's: the development was irregular and slow; no medium was found reliable and satisfactory. Material transferred to fresh agar slopes for subculturing often failed altogether or only developed, possibly after weeks or even months, so slowly that the strain could only be maintained by preparing numerous parallel subcultures. Working with cultures very kindly sent to us repeatedly by Prof. W. Vischer, we could confirm his observations and encountered the same difficulties. It testifies to the author's experience and patience that in these circumstances he obtained pure cultures at all, quite apart from keeping them going for years. Vischer's and our own observations suggested that the unsuitability of all the media employed was due to a specific factor, probably not a nutritional deficiency, e.g. lack of a mineral element or accessory substance. Addition of soil, or meat, or yeast extract, for instance, did not improve the growth sufficiently to suggest that these substances provided any essential ingredients for healthy development like that in the natural habitat.

Microscopical investigations indicated pathological alterations of the cell contents. Certain phenomena pointed in the direction of osmotic disturbances. Vischer's cultures with 2% dextrose were slightly better than the rest, a difference which was not attributable to the nutritive value of sugar. When, to enhance the chance of success, a larger piece of cell material was transferred to a new agar surface, only the inner portion survived. From this cells crept out to colonize the substratum, while the outer part died. Vischer's advice (in a letter) to let the agar surface dry slightly before inoculation points in the same direction.

These considerations were supported by Geitler's (1944) ecological and cytological observations, showing that *P. cruentum* grows in places which, though humid, are protected from the immediate effects of rain and running water (p. 323), and that the cells contain little water and burst when moistened. 'An appearance true to nature is only observed when the cells are inspected in their own mucilage without addition of water or in 10–15 % solution of sucrose' (p. 302, transl.).

Our conclusion and working hypothesis was that cultural media should be supplemented with substances increasing their osmotic pressure.

II. MEDIA WITH INORGANIC SALTS

Our earlier attempts with a great variety of media, either using material from the walls of a greenhouse (where it was abundant to the extent of being a nuisance) or with cultures repeatedly sent to us by Vischer, were not encouraging. Only one culture in 1935 with a relatively high concentration of nutrient salts in agar showed a little spreading and multiplication. Unfortunately, this success was not followed up.

Experiments were commenced again in January 1948, and this time an agar medium was used containing soil extract and artificial sea water, not supplemented with nitrogen or phosphorus. The composition of the sea water was: NaCl 3 %; MgCl₂ 0.4 %; KCl 1 %; MgSO₄·7H₂O 0.5 %; CaSO₄ 0.1 % (Pringsheim, 1946, p. 28). After only 1 day cells had begun to move out of the inoculum into the free agar surface, where their tracks could be seen with a hand lens. After a few weeks a pink spot had developed. The growth could be further improved by adding Beijerinck's solution (Pringsheim, 1946, p. 35), even 1/10 of the normal concentration making a marked difference.

When natural instead of artificial sea water was used no appreciable improvement was seen, provided that soil extract was present. By varying the concentration, about 1/2 of the original concentration of artificial sea water was found to be optimum, 1/1 and 1/4 slightly less favourable, 1/8 and 2/1 not quite so reliable, while without any addition no spreading and only poor and irregular development was obtained.

Agar could be replaced by filter paper and less satisfactorily by cotton-wool, cellulose wadding, plaster of Paris, or porous porcelain. Without any solid substratum, in dilute natural or artificial sea water with nutrient salts and soil extract only, growth was slow and poor, but apparently better than in Vischer's (1935, pp. 81–2) liquid medium.

Attempts were made to replace the mixture of salts by single ones. Sodium chloride, magnesium chloride, potassium nitrate and calcium nitrate in concentrations of 0.5, 1, 2 and 3 % all failed to give any better results than media without these additions. There was no spreading; the growths were confined to dark red colonies of a few mm. in diameter.

In media, otherwise suitable, but with a relatively low concentration of nutrient salts, deficiency is revealed after a period of months by the colour changing from red to brown. The red hue can be restored by addition of a mineral nutrient solution but not by an iron salt. A nutrient solution with 0.1 % ammonium nitrate prevents this change of colour into brown.

The experiments with salts show that the favourable influence of sea water on the creeping and multiplication of *Porphyridium* is not simply due to its osmotic effect. This conclusion is confirmed by the experiments with organic substances.

III. THE EFFECT OF ORGANIC SUBSTANCES

Kufferath (1920, 1930, p. 180) used various organic salts without apparent favourable results. The only medium, in which he seems to have obtained colonies, was an agar containing 0.5% asparagin. The colonies were isolated, so the medium did not permit creeping. Vischer (1935, p. 88) observed a growth-promoting influence of asparagin and glycine. He (pp. 89 sqq.) also obtained a slightly better growth after the addition of 2% dextrose to his standard medium containing 0.1% glycine and dilute mineral salts.

In our experiments neither sucrose nor dextrose in concentrations of 2, 4 or 6%, nor glycerine at 1 or 2% could replace sea water, even if 0.2% NaCl was present. Dextrose in sea water showed no favourable influence on the growth; on the contrary, spreading was considerably less. A higher percentage of agar, e.g. 3%, also reduced the creeping of cells. On slightly alkaline 8% gelatine with sea water no growth at all was obtained.

Addition of 0.05–0.2% Difco yeast extract to sea water-Beijerinck solution has no distinct effect, while soil extract, 0.1% glycine, or 0.2% Difco tryptone (peptone), renders the growth more vigorous and longer lasting. Vischer (1935, p. 88) obtained no good results with peptone, but he may have used Witte's peptone which is unsuitable for many micro-organisms.

The favourable influence of 0.2–0.5% tryptone is especially marked in liquid media, for instance, artificial sea water with Beijerinck solution 1/4. Without the addition of inorganic nitrogen there develops only a slight growth which soon becomes brown. 0.1% agar as supplement to a sea water-Beijerinck solution has no distinct enhancing effect.

The best liquid medium so far for *P. cruentum* is therefore sea water (natural or artificial) + Beijerinck solution 1/2 + Difco tryptone 0.2%. In 3–4 weeks a dense red mucilaginous growth is formed.

IV. APPEARANCE OF THE GROWTHS

While on agar without sea water the alga develops but slowly, if at all, and eventually appears only as small, tough, gelatinous, blood-red colonies, on sea water agar spreading is observed, according to light and temperature conditions, after 1 or 2 days, and multiplication goes on steadily until first pink, then carmine red films cover the substratum, the edges being denser than the rest.

It is not easy to decide whether the healthy, luxuriant growth in the latter case is due to the distribution of the cells over a greater area of the medium, or whether there is an immediate favourable influence of the salt mixture on cell multiplication. Although a dense growth, appearing like drops of blood, may develop without sea water, the great difference in reliability and quantity of subcultures is best explained by an improvement of the conditions for multiplication by such salt mixtures, an improvement also indicated by the healthier state of the cells.

Spreading can best be observed when portions of a dark red film are transferred to agar with sea water. The paths of the cells can be seen with a hand lens (cf. Vischer, 1935, p. 80). The cells turn towards the light, so that, when the tube stands on a window-sill with the free agar surface towards the light, or is illuminated obliquely from above by an electric lamp, the growth-covered area of the slope has a fan-like shape (Fig. 1). Positive phototaxis, already observed by Vischer (p. 79), is so strong that, when the tubes are unilaterally illuminated, it causes the cells to creep along the inner glass surfaces (Fig. 2). The growth

may eventually be found mainly on the glass, where the cells use the mucilage they have themselves excreted as a substratum for movement. The water film between the glass and the agar, often the seat of considerable growth in species of *Euglena* and other organisms, is not sought out by *Porphyridium*, which also does not penetrate into the agar unless it is very soft.

In liquid media growth starts on the bottom where the cells can be seen with a lens, almost evenly distributed over the inner surface of the hemispherical part of the test-tube. Later on a mucilaginous film covers almost the whole glass surface with its greatest density where the illumination is greatest, i.e. on the side away from the source of light. Thriving cultures have, in addition, a red ring near the surface of the fluid. Most of the growth sinks eventually to the bottom.

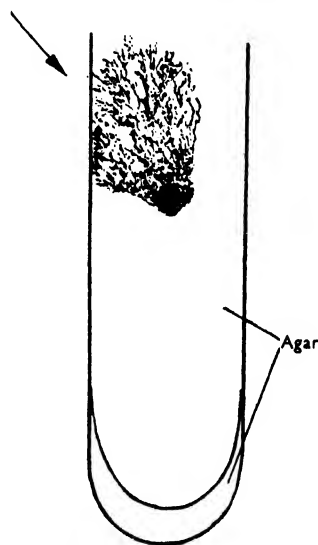


Fig. 1. Fan-shaped growth on agar slope, the light coming from the left as indicated by the arrow.

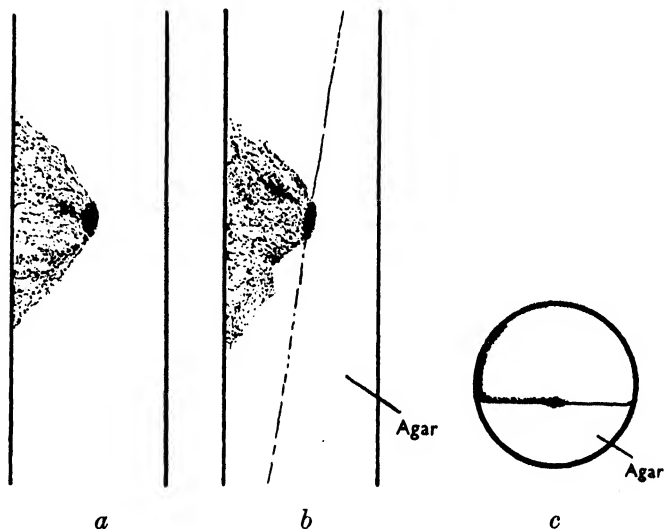


Fig. 2. Growth on agar creeping over the surface of the glass: (a) from front; (b) from side; (c) cross-section diagrammatic. Illumination horizontal.

V. THE MOVEMENT

Vischer (1935, pp. 78-9) speaks of naked cells with an amoeboid movement. He observed slightly irregularly shaped 'amoeba-like' cells, an expression already used by Rosenvinge (1929, p. 72). Geitler (1944, p. 316) challenges this description as incorrect and doubts whether Vischer's observation, that swarming cells burst on light pressure, proves that they lack a cell wall. He claims to have found cell walls in every case, but Vischer (private communication) could not observe any in such burst cells, and believes that Geitler may not have seen the right type of wandering cells.

Geitler describes the cells as slightly ellipsoid with the long axis in the direction of the movement, while the location of the excentrically placed nucleus has no relation to the shape and direction of creeping cells and is only decided by the axis of division.

In our cultures healthy cells were almost completely spherical and showed no correlation between direction of movement and position of the nucleus. That could best be seen on agar plates. No indication of changes of shape during locomotion was observed. The

existence of cell walls in wandering cells could neither be established beyond doubt nor ruled out altogether. Plasmolysis could not be obtained, but only an irregular contraction to a more or less ellipsoid shape. Cells burst by pressure remained spherical while contents flowed out; but no distinct cell wall could be seen.

Geitler (1944, p. 321) explains the movement as due to the excretion of mucilage and figures (p. 308, fig. 3; p. 319, fig. 9) gelatinous stalk-like strands, ending at a short distance from the cells by tapering out to sharp points. They were directed away from the light and connected with envelopes surrounding the bodies. Mucilaginous stalks had already been observed by Vischer (1935, p. 70, fig. 1), who, however, uttered a warning against confusion of the slight passive locomotion caused by these exudations with the active movement of amoeboid reproductive cells. Geitler, if we understand him correctly, makes a similar distinction between the displacement of cells by extending mucilage and the active movement of swarming cells by excretion.

We saw short, relatively wide stalks as figured by Vischer, and narrow long ones like Geitler's, but tend to share the former's opinion that none of these exudations can cause more than a slight pushing outwards of cells from the gelatinous mass after transference from a relatively dry to a damper substratum. In liquid media the whole of the mucilage containing and holding together the red cells, may consist of such strands. Often eight or even sixteen cells are bound together by them in a similar way to that in *Interfilum*, *Dictyosphaerium* or *Cosmocladium* (Fig. 3). The older portions of the strands, although still

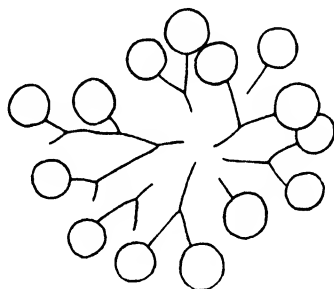


Fig. 3. Colony from liquid medium showing strands of mucilage as observed in the living state without staining. $\times 1000$.

possessing some coherence and holding the colony together, may be invisible without special treatment, so that the younger parts directed towards the centre of the colony seem to end in points as described by Geitler.

The movement, as already stated by Geitler (1944, p. 317) is too slow to be immediately perceived under the microscope. That of unicellular spores of other Bangiaceae is quicker, while the movements of Florideae are generally very sluggish (Rosenvinge, 1929, pp. 72, 75, 78). In *Porphyridium* it takes at least 1 min. to detect that cells have shifted from their original position, while in *Erythrotrichis* the velocity 'is often so great that the movement is easily directly perceivable' (Rosenvinge, 1929, p. 74).

The kind of motility, however, is evidently the same. The monospores and carpospores of Bangiaceae are described by Rosenvinge (1929, pp. 73-4) as 'globular with one distinct central star-shaped red chromatophore, in the centre of which a...pyrenoid is visible. The nucleus is situated in a notch of the chromatophore and is therefore only visible in the living cell when it is situated in a horizontal plane through the centre. The spores are not

amoeboid, but nevertheless show conspicuous sliding movement... constantly in contact with the slide; it shows resemblance with the movement of the Diatoms. The advancing movement may be combined with a rotation on a vertical axis... It is not always the same point of the sliding spore which is in contact with the substratum, but the movement is never rolling.' Structure and locomotion of *Porphyridium* cells might be described in exactly the same way. Tetraspores and carpospores of other Rhodophyceae are also spherical and very similar.

Like the earlier observers we did not find it possible to ascertain a definite physical force responsible for the movement of Rhodophycean cells. The mucilage is no doubt essential, but it is controversial whether it can provide the mechanical means by which the cells are pushed along. With Rosenvinge (1929, p. 79) we believe: 'The efficient cause must probably be sought in a special action of the protoplasm where it is in contact with the substratum.' This is, of course, no physical explanation, but the mechanism of no gliding movement of lower organisms, whether Myxophyceae, Beggiatoaceae, Achromatiaceae of Myxobacteria, is really any better known. It must be sufficient for the time being to align that of the Rhodophyceae with that of the others, and to distinguish it from the movements of *Chrootheca* (Pascher & Petrová, 1931) and Desmids effected by swelling mucilage, and also found in *Porphyridium*, and from that of Diatoms too which are differently organized, although it is also possible that Geitler is right and the movement is due to excretion.

VI. DISCUSSION

The fact that *P. cruentum* is adapted to a higher salinity than that suitable for freshwater algae has certainly an ecological bearing but it may also be connected with the taxonomic status of the species. Not only are the Bangiaceae, to which *Porphyridium* belongs, in some part marine or brackish water forms, but one species described by Kylin (1937, 1943) as *P. marinum*, and according to him easily grown in culture, is at least very similar to, perhaps even identical with, *P. cruentum*. Kylin's diagnosis gives no feature not fitting to the latter. Unfortunately, the cultures were lost by an accident, so that no real comparison has been possible.

One may imagine that *P. marinum* was somehow transported to places far from the sea, and found a new habitat on walls and in greenhouses in a similar way to that in which flowering plants from seashores came to grow at ruderal localities where the salt content was higher than in other places. The parallel may even go further in the transport being effected by man in both cases. The habitats of *P. cruentum* point in this direction, since they never seem to be far from human habitations (Geitler, 1944, p. 322).

A favourable influence of salt mixtures on algae living far from the sea is not restricted to this instance. *Euglena obtusa* Schmitz, 1884 (syn. *E. deses* Bracher, 1919; *E. limosa* Gard, 1922), a species of periodically flooded brackish mud, which we observed in large masses near Flatford Mill Field Centre, nr. Colchester, was also found, though in small numbers, in a very dirty, periodically half-dry pool at Cherryhinton, nr. Cambridge. Another Euglenoid species, occurring in similar habitats, and likewise abundant on Flatford mud flats, is *Eutreptia viridis* Ehrenb. We found it several times in relatively small numbers in mud and on dead leaves in a polluted ditch near Jesus College, Cambridge. Unlike *Euglena obtusa*, the only Eugleninean which we were not able to grow in culture, *Eutreptia viridis* multiplies in unialgal cultures with soil and water, but it never thrives. Satisfactory cultures were, however, obtained, when about a quarter to a half strength

sea water was added. While *Euglena* is mainly a fresh-water genus, species of *Eutreptia* (including *Gymnastica* Schiller and *Eutreptiella* da Cunha) are only recorded from brackish and sea water with the exception of a few doubtful records, and of *Eutreptia viridis* which, like *Porphyridium cruentum*, though mistaken for a fresh-water form, is really adapted to salt water also.

A different case is afforded by the three main fresh-water species of *Cladophora*. As Mr E. A. George found in our laboratory, *C. fracta*, and to a lesser degree *C. glomerata* and *C. crispata*, are favoured by an addition of sea water to the medium. In nature they penetrate into brackish habitats and can withstand the change in salinity caused in estuaries by the tides, in the same way as *Vaucheria piloboloides* and *V. thureti*. Very few other algae are thus adaptable, and consequently there does not seem to exist anywhere a rich tidal brackish-water algal flora. Brackish conditions exclude most Diatoms, Myxophyceae, and other epiphytes besetting *Cladophora* and *Vaucheria*, and the improved growth in cultures when sea water is added may be due in some part to the reduction of competition.

There is in *Porphyridium cruentum* some connexion between the presence of a balanced mixture of salts and the exhibition of gliding motility, although no explanation has so far been found. If this movement depended on the presence of a certain ion, for instance, for the swelling of a transporting mucilage, a single salt should be sufficient to activate it. The necessity for a balanced mixture like sea water renders more probable a direct relation between the movement and a certain state of the protoplasm itself.

Microscopic inspection does not give any help towards a mechanical explanation. Comparison with amoeboid motility is not supported by evidence, nor is there any indication of a similarity with the movement of Diatoms. The nearest in appearance, apart from other Rhodophyceae, are the movements of unicellular Myxophyceae and Myxobacteria. Rosenvinge (1929, p. 79) seems to assume that motile cells of Rhodophyceae have no cell wall and therefore believes theirs differ from the 'sliding movement... in the Cyanophyceae (Myxophyceae), the Myxobacteria and some true Bacteria... where the protoplasm is separated from the substratum by the membrane unless the existence of an extra-membranaceous layer of protoplasm may be supposed'. This is not quite clear. If a membrane is different from the protoplasm proper mainly by its density, every cell has one. If membrane means a cell wall, i.e. a covering layer different from the protoplasm in its physical properties and chemical composition, then probably Myxobacteria have none, whilst it does exist in *Porphyridium*.

Comparison with cells of higher plants may be misleading, since, except in some Myxophyceae, so little is known of the fine structure of covering layers in these lowly organisms. Although the organization of a *Porphyridium* cell with its nucleus, chromatophore, and pyrenoid is much the same as that of other algae, while Myxophyceae and Myxobacteria have no such differentiation, the kind of movement seems to be similar. This is especially the impression given by unicellular Myxophyceae like *Chroococcus*, *Aphanothece*, *Synechococcus*, and *Tetrachloris* which we have been able to compare in cultures. Phototaxis, however, was only observed in *Merismopedia* and *Holopedia*, where the cell shape is more different.

The effects of organic substances, H-ion concentration, temperature, and light intensity on *Porphyridium cruentum* are not very marked. This is in accordance with observations in nature by Vischer and Geitler. In some of the habitats pollution by organic substances

was strong, in others nil. They were also different in light intensity, temperature and humidity, so that no definite conclusions as to the needs of the alga could be drawn (Vischer, 1935, p. 70; Geitler, 1944, p. 323). All the habitats seem, however, to have one characteristic in common: changes in dampness and a relatively high salt concentration.

VII. SUMMARY

Porphyridium cruentum, up to now only cultivated with difficulty, thrives healthily when at least 25 % of sea water is added to a mineral agar medium. The improvement reveals itself first by the active gliding movement of the cells, followed by abundant multiplication. In liquid media with sea water growth is improved by the addition of peptone and may then be considerable.

The ecological and physiological implications of this phenomenon are discussed and other instances are recorded in which algae, living far from the sea, are favoured by an admixture of sea water.

We are indebted to Dr F. M. Haines, Queen Mary College, London, for correcting the manuscript.

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STATISTICAL TEST FOR OPTIMAL CONDITIONS: NOTE ON A PAPER OF EMMETT AND ASHBY

By G. H. JOWETT AND G. SCURFIELD, *The University, Sheffield*

In their paper 'Some observations on the relations between H-ion concentration of the soil and plant succession', Emmett & Ashby (1934) proposed a sampling method for separating the frequency distribution of a species over an area from that of soil acidity over the same area.

It is unfortunate that the statistical test used in the analysis of their data was incorrect and consequently the hypothesis that the two species *Pteridium aquilinum* (L.) Kuhn and *Vaccinium myrtillus* L. occurred with the same frequency at every pH value within their respective pH ranges was accepted when in fact there is significant evidence to the contrary.

We propose to discuss in detail the data which were given in Table 1 of that paper, and are reproduced in Table 1 below.

Table 1. *Frequency distribution of occurrence of Pteridium and Vaccinium in classes of pH*

pH class means	No. of samples	Frequency of		Percentage occurrence of	
		<i>Pteridium</i>	<i>Vaccinium</i>	<i>Pteridium</i>	<i>Vaccinium</i>
4.8	2	0	2	0	100.00
4.9	2	0	2	0	100.00
5.0	2	0	2	0	100.00
5.1	5	1	4	20.00	80.00
5.2	13	6	8	46.15	61.54
5.3	17	8	11	47.07	64.71
5.4	7	4	3	57.14	42.86
5.5	44	27	28	61.36	63.64
5.6	78	41	54	52.56	69.23
5.7	16	5	12	31.25	75.00
5.8	7	5	1	71.43	14.29
5.9	9	4	3	44.44	33.33
6.0	7	5	1	71.43	14.29
6.1	3	2	0	66.67	00.00

In the test used by Emmett & Ashby, the expected frequency of *Pteridium* in each pH class was calculated on the assumption that the species was present in 51.772% of the samples falling in that class. The figure 51.772 is the mean of the non-zero entries in column 5 of Table 1. Then after grouping the lowest four classes together, and the highest

four classes together, they calculated the sum $\sum \frac{(f_0 - f_e)^2}{f_e}$ (f_0 = observed frequency of *Pteridium* and f_e = the expected frequency), and compared it with the distribution of χ^2 for 7 degrees of freedom, this being one less than the number of terms entering into the summation. Since it was very nearly the same as the 50% point of the distribution, they concluded that there was no evidence for rejecting the null hypothesis.

There are two main criticisms of this test:

(1) The summation does not include terms arising from differences between observed and expected frequencies in samples not bearing *Pteridium*. The correct value of χ^2 is

actually 13.72, more than twice the value obtained by Emmett & Ashby; this value lies between the 5 and 10% points of the distribution, and throws some doubt on the null hypothesis, though not sufficient for its rejection.

(2) The test itself, even supposing it to be correctly carried out, is not the most powerful test available. It takes no account of the fact that the pH classes are ordered, and tests the null hypothesis against an unnecessarily general class of alternative hypotheses. As a result, the test fails to show that the null hypothesis is disproved.

A more powerful test would have for its null hypothesis: the pH values of quadrats bearing *Pteridium* but not *Vaccinium* form a random sample from the same population as those of quadrats bearing *Vaccinium* but not *Pteridium*. Rejection of this hypothesis implies rejection of the original hypothesis, since when one species is present on a particular quadrat the other is usually absent. If the populations do differ, the test should be particularly sensitive to differences in their means. Such a test is the 't test' of Student, subject to the normality of the populations of acidities sampled.

Actually, the evidence suggests that the population is bimodal, a fact indicative of statistical heterogeneity in the sample. An investigation of this would be a desirable preliminary to the application of any statistical test, but since this is not possible here the 't test' will be applied to the data available to demonstrate its greater power. The departure from normality is not serious, and the test may be taken to apply approximately at least. Though Table 1 is not as complete as might be desired for this purpose, it is possible to make a reasonable guess at the missing information. We shall assume that where corresponding entries in the third and fourth columns total more than the entry in the second column the discrepancy is due to the occurrence of both species on a quadrat, and further, that there is a minimum number of occurrences of this kind. The reconstructed information is given in Table 2.

Table 2. *Frequencies of occurrence of Pteridium only, Vaccinium only, both species and neither species, in classes of pH*

pH class means	No. of samples	Frequency of		Both species	Neither species
		<i>Pteridium</i> only	<i>Vaccinium</i> only		
4.8	2	0	2	0	0
4.9	2	0	2	0	0
5.0	2	0	2	0	0
5.1	5	1	4	0	0
5.2	13	5	7	1	0
5.3	17	6	9	2	0
5.4	7	4	3	0	0
5.5	44	16	17	11	0
5.6	78	24	37	17	0
5.7	16	4	11	1	0
5.8	7	5	1	0	1
5.9	9	4	3	0	2
6.0	7	5	1	0	1
6.1	3	2	0	0	0

The mean pH for the quadrats with *Pteridium* only is 5.585, while that for those with *Vaccinium* only is 5.485; the difference is 0.100 and its standard error 0.035, based on 173 degrees of freedom. If the null hypothesis is true, the ratio of the difference to its standard error is distributed as *t* with 173 degrees of freedom (Fisher, 1944). The observed ratio is 2.85, a value greater than the 2% point of the distribution of *t*. Hence, we may

conclude that in the restricted habitat investigated, *Pteridium* prefers soils of relatively high pH as compared with those preferred by *Vaccinium*.

Having established the existence of the effect, we would wish to investigate its magnitude. The fitting of curves, similar to dosage-mortality curves, using the probit or angular transformations (Fisher & Yates, 1947) to show the effect of increasing pH on the percentage occurrence of each of the two species would be of interest, as shown in Jowett & Scurfield (1949).

Finally, while we appreciate that the incorrectness of the statistical method used by Emmett & Ashby may have been noted, no record has come to our notice. In view of this, and of the value of the experimental technique which they pursued, as shown in Jowett & Scurfield (1949), we consider the above criticism as being necessary.

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A STATISTICAL INVESTIGATION INTO THE DISTRIBUTION OF *HOLCUS MOLLIS* L. AND *DESCHAMPSIA* *FLEXUOSA* (L.) TRIN.

BY G. H. JOWETT AND G. SCURFIELD, *The University, Sheffield*

(With five Figures in the text)

1. INTRODUCTION

Gleason (1926) describes a natural plant community as 'representing the selection of a certain environment acting on a given population of species'. In a climax community it is to the local variation in this environment itself that some at least of its internal vegetational variation, that is, variable success and incidence of its constituent species, is attributable. Further, the incidence of a definite type of plant community (which implies incidence of its characteristic species, e.g. *Calluna* in heathland) appears in some cases to correspond to the distribution of some environmental factor, e.g. heathland on acid sandy soils (Ashby, 1935). It appears probable, therefore, in cases where the incidence and success of a species appears to be noticeably correlated with variations in some environmental factor, that a quantitative investigation into the causes of such variations as they occur locally, together with some means of assessing the relative importance of the effects of such causes on local distribution and success of the species investigated, could be used to predict the wider incidence and success of such species in respect to this factor. Anything which enhances a knowledge of the physiological requirements of the species will increase the accuracy of any prediction of the habitat best likely to meet these requirements. For example, the wider the range of local variation in the factor investigated, and the closer the analysis of the causes of this variation, the more likely is the prediction of distribution and success, drawn from local investigations, to be correct. As for the causes which cannot be investigated locally, e.g. climatic variation, their effects can often be predicted qualitatively from experience.

Generally, it is the edaphic factor which is the primary environmental factor influencing species success and distribution in a given climatic area, and since its influence can be approximately assessed from determinations of pH, organic content, and moisture content—in themselves easily determinable functions of a wide range of heterogeneous effects, such as slope, incidence of tree cover, exposure, base exchange capacity, and the like—it is the factor which will be considered in assessing the value of the above conclusions.

We may point out here the essential similarity of the above concept to that which has led Boyko (1947) (of whose latest paper we were unaware at the time of our experiments) to his conclusion: 'The specific topographical distribution (micro-distribution) of an ecotypic plant species is a parallel function of its general geographical distribution (macro-distribution), since they are both determined by the same ecological amplitudes.' Boyko is dealing with the variables which together constitute climate, and while we appreciate his conclusion, we can commend a more rigorous analysis of the results.

1.1. The following experiment, then, is a preliminary attempt to assess the relative importance of the effects of the causes of local edaphic variation on local distribution and success of *Holcus mollis* and *Deschampsia flexuosa*. From the results we shall attempt to

predict the wider distribution and success of these species, and in so doing suggest a first approach to the more complex problem defined by Watt (1947*a*): 'an elucidation of the dynamic relations which hold between one species and another and in the plant community itself'.

Locally, *Holcus mollis* L. and *Deschampsia flexuosa* (L.) Trin. occur as associates in nearly all steep woodlands in the Sheffield area, and ecological observations therein (Scurfield, 1949) have confirmed the conclusions of Pearsall (1938*a*), from Lakeland and Yorkshire woods, of Watt (1931), from Scottish beechwoods, and of Woodhead (1906), from Huddersfield Pennine woods.

2. DESCRIPTION OF EXPERIMENTS

2.1. The woodlands investigated were chosen so as to give as wide a range of type as was consistent with ease of accessibility to Sheffield, and included the following:

(a) Ecclesall Beech-Chestnut-Oakwood: a Coal Measure woodland, with areas of sandstones and shales. Altitude 350–550 ft.; slight south-eastern slope; approximately 4 miles south-west of Sheffield.

(b) Limb Brook Valley Beechwood: in the transition zone between the base of the Millstone Grit and the Coal Measure region; essentially sandstone. Altitude 700–900 ft.; steep south-western slope; about 1 mile north of (a).

(c) Lady Canning's Pine-Sorbus Plantation: a wood retrogressing to *Calluna*-heath at the base of the Millstone Grit Plateau. Altitude about 1100 ft.; slight northerly slope; nearly 5 miles west-south-west of Sheffield.

(d) Totley Oak-Birchwood: a Coal Measure type on sandstone. Altitude 500–600 ft.; slope steep north-westerly and facing (a) above.

2.2. For the collection of numerical data, the method used was essentially that of Emmett & Ashby (1934). Transects were drawn through the woodlands selected, at a fixed equal distance apart, the distance being based on the size of the woodland and selected arbitrarily beforehand as that giving the appropriate number of samples. At arbitrarily fixed equal distances (also selected previously) along each transect, soil samples were taken, irrespective of the presence or absence of *Holcus mollis* or *Deschampsia flexuosa*, of the top 10 cm. of the profile, and the following determinations carried out on them: pH, moisture per 100 g. dry weight, and loss on ignition for 100 g. dry weight (as a measure of organic content). In practice, the selected distance separating the transects (say 25 yards) was paced out roughly with no regard to the unevenness of the ground; the same applies to the chosen distance down each transect. The flora on a square-metre quadrat surrounding the point sampled was recorded. As an estimate of success, the yield in grams fresh weight was obtained by cropping the *Holcus* and *Deschampsia* over the same area. The analysis of the yield results will be presented later.

As the number of determinations was large, and because of the difficulty of transport of large blocks of undisturbed soil, as recommended by Pearsall (1938*a*), the soil samples were rapidly mixed and transported to the laboratory closely packed in large glass tubes, moisture and pH determination being made as soon as possible after arrival. The glass electrode method of pH determination was used throughout, with a 2:1 water:soil ratio. In view of the potential drifts observed by Pearsall (1938*a*) with disturbed soil samples using the quinhydrone method, the pH results may perhaps at this stage best be regarded as comparable laboratory results rather than ecological values.

The later part of the drought month of August 1947 provided the opportunity for collecting samples, and the complete absence of rain makes all moisture determinations, both between and within woodlands, comparable, whilst also providing information as to the shading effect of *Pteridium*, etc.

3. ANALYSIS OF EXPERIMENTAL RESULTS

3.1. Acidity and distribution

3.11. Earlier observations, notably those of Olsen, Atkins and Salisbury, on the effects of acidity on species distribution are criticized by Emmett & Ashby, who point out the necessity of collecting the data in such a way that the frequency distribution of soil acidities may be separated from the frequency distribution of the species in relation to soil acidity. Dealing with *Pteridium* and *Vaccinium*, Emmett & Ashby concluded 'that there is an equal chance of finding these species at any soil pH within the species range of soil acidities investigated'. A more critical statistical analysis has been applied to their data (Jowett & Scurfield, 1949), and shows that this conclusion is in fact not justified. The following analysis will be on the lines suggested by us (1949), with some endeavour to formulate the problem in precise statistical terms.

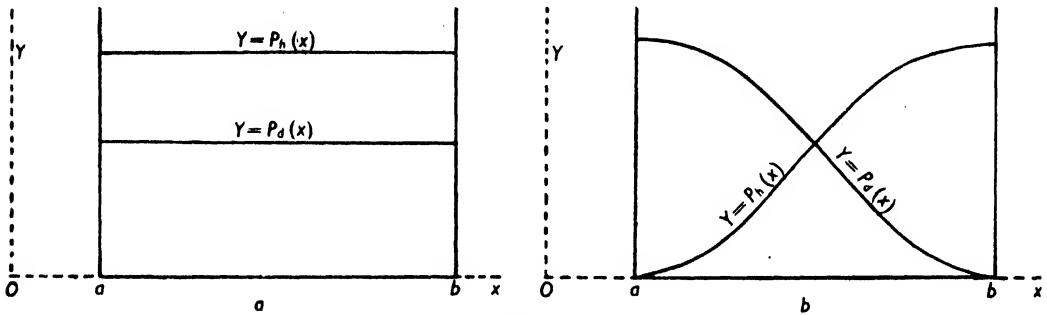


Fig. 1.

3.12. Suppose that in a particular wood the probability of *Deschampsia flexuosa* occurring on a quadrat, the pH value of which is x , is a function $P_d(x)$ of x . This function will be assumed to be small or zero for relatively small x , to increase with x to a stationary maximum value, and then to decrease, as x increases still further, to a small or zero value. A similar kind of probability function $P_h(x)$ will be assumed to exist for *Holcus mollis*, and the occurrence of each species assumed to be in no way directly dependent on that of the other. The range outside which $P(x)$ is negligible is the 'pH range' of the species in the habitat investigated.

3.13. The wood itself will have a range ($a < x < b$) outside which pH values rarely occur, and a quadrat selected at random therein will have a definite probability $f(x)$ of yielding a pH determination x . Of the possible theoretical relationships which might exist between $P_d(x)$ and $P_h(x)$ within this range, our data suggest consideration for practical purposes (see § 3.17) of only the two following possibilities:

(a) $P_d(x) = \text{constant}$; $P_h(x) = \text{constant}$ ($a < x < b$).

(b) For some fixed value x_0 of x , $P_d(x) > P_h(x)$ ($x < x_0$); $P_d(x) < P_h(x)$ ($x > x_0$); or vice versa.

These possibilities correspond roughly to the situations shown in Fig. 1.

3.14. If a sample of quadrats be selected at random from the wood, those bearing *Deschampsia* but not *Holcus* will be a random sample from the population the frequency function of which is $f(x) P_d(x) (1 - P_h(x))$, whilst those bearing *Holcus* and not *Deschampsia* will be a random sample from the population $f(x) P_h(x) (1 - P_d(x))$. These populations will have different means if alternative (b) above is true, and conversely. Hence, the application of Student's 't' test to the two subsamples just described will decide between the two alternatives; unless the distributions show signs of violent skewness, it can be taken to apply approximately at least.

3.15. Actually, the assumptions made above respecting the functions $P_d(x)$ and $P_h(x)$ are only approximately satisfied. Thus, since reproduction of both species is predominantly vegetative under the conditions being considered, the probability of *Holcus*, for instance, occurring in a quadrat may depend to some extent on the presence or absence of *Deschampsia*; also, the transect method of sampling does not provide samples behaving quite as random samples partly because of the over-dispersion (Blackman, 1942) resulting from this vegetative reproduction, though as yet we have not succeeded in finding any more satisfactory sampling procedure. Nevertheless, the degree of approximation is such that valid conclusions can be drawn from the data.

Table 1. *Differences in mean pH between quadrats bearing Deschampsia and quadrats bearing Holcus*

Wood	Quadrats bearing <i>Deschampsia</i> but not <i>Holcus</i>		Quadrats bearing <i>Holcus</i> but not <i>Deschampsia</i>		Student's 't test' values	Level of significance
	No.	Mean pH	No.	Mean pH		
Totley	29	3.997	61	4.109	1.84	$0.05 < p < 0.10$
Limb Brook	37	3.810	48	3.999	3.76	$p < 0.005$
Ecclesall	25	3.737	41	3.918	3.45	$p < 0.005$
Lady Canning's	31	3.664	3	4.345	4.79	$p < 0.005$

3.16. In Table 1 are given the results of a preliminary analysis of the data using Student's test. These results establish as real the difference between the mean pH values for quadrats bearing one species but not the other in all woods except Totley Oakwood, where the existence of a difference, though not established, is definitely suggested. In all cases *Deschampsia*-bearing quadrats have a lower mean pH than those bearing *Holcus*. Hence, there is good reason to believe that alternative (b) of § 3.13 is true in all cases.

3.17. It remains to determine as precisely as possible the forms of the curves $P_d(x)$ and $P_h(x)$ within the range of pH established for each wood, to determine their point of intersection x_0 , and to estimate the common value of $P_d(x)$ and $P_h(x)$ at that point of intersection. The frequencies and percentages of occurrence on which this analysis will be based are given in Table 2.

In all cases it was assumed that over the pH range of the woods the functions $P_d(x)$ and $P_h(x)$ were capable of approximate representation by sigmoid curves of the probit (cumulative normal) type. Such curves were fitted by the method suggested by Finney (1947) and are shown in Figs. 2 and 3, together with the percentages on which they were based. In some cases, the observed percentage points at the extremes of the ranges show rather large deviations from the curves, but since they are based on very small samples, they are not as serious as they appear to be. A test of goodness of fit was carried out for each curve fitted, and in no case did the value of χ^2 obtained exceed the 10% level of significance; the total value of χ^2 for all six curves was 14.82 for 12 degrees of freedom,

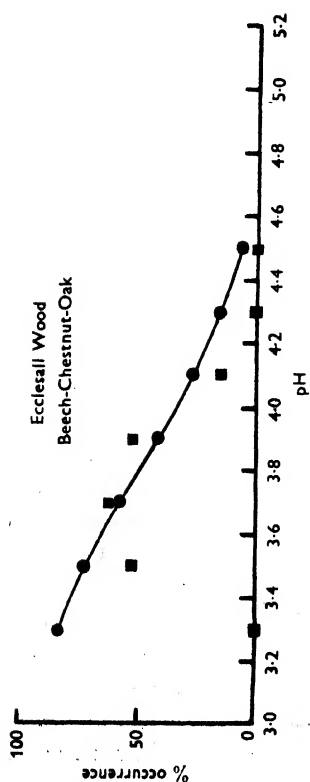
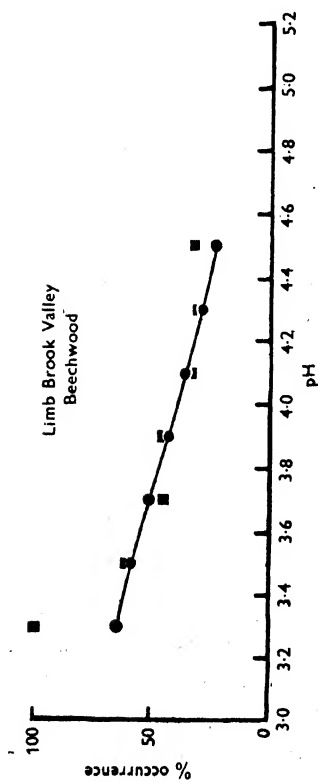
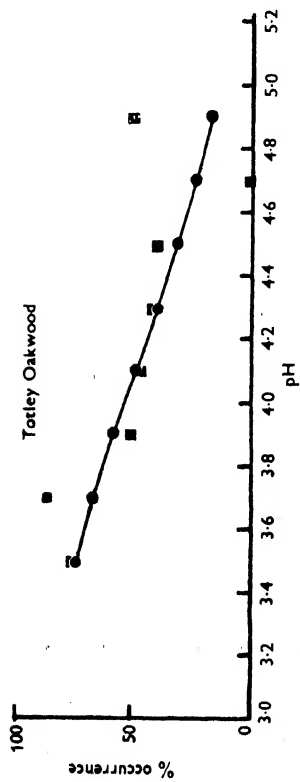


Fig. 2. Percentage occurrence of *Deschampsia* for varying pH.

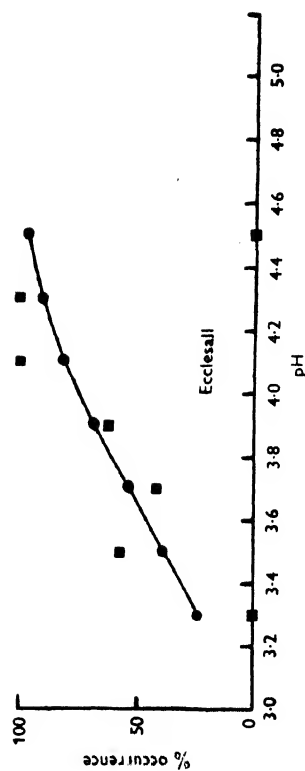
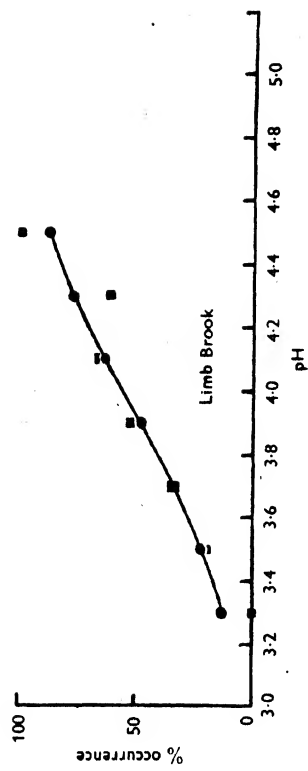
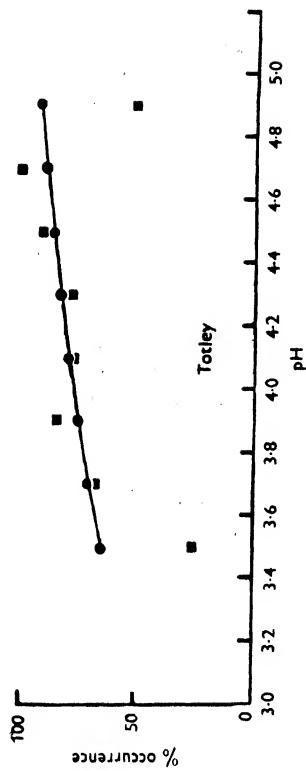


Fig. 3. Percentage occurrence of *Holcus* for varying pH.

a value between the 50 and 30% points of the distribution. While this test was not very sensitive in the individual cases owing to the need for combining classes to avoid small expected frequencies, it none the less affords evidence of the goodness of fit of the sigmoid curves on the whole; hence, the assumption made in § 3.13 appears to be fully justified. We may note here that an admissible alternative test to that of 3.14 would consist of a comparison of the values of σ for the fitted curves $P_d(x)$ and $P_h(x)$; however, the test given in § 3.14 is slightly more general in character, and certainly powerful enough for its purpose. The estimated points of intersection of the curves are given in Table 3.

Table 2. *Frequency and percentage occurrence of Holcus and Deschampsia*

pH range	% frequency of occurrence of			% occurrence of	
	<i>Holcus</i>	<i>Deschampsia</i>	No. of samples	<i>Holcus</i>	<i>Deschampsia</i>
Totley Oakwood					
3.40-	1	3	4	(25)	(75)
3.60-	10	13	15	67	87
3.80-	33	20	40	83	50
4.00-	23	14	30	77	47
4.20-	17	8	22	77	36
4.40-	9	4	10	90	40
4.60-	1	0	1	(100)	(0)
4.80-	1	1	2	(50)	(50)
4.99					
Limb Brook Valley Beechwood					
3.20-	0	2	2	(0)	(100)
3.40-	2	6	10	20	60
3.60-	9	12	27	33	44
3.80-	17	15	33	52	45
4.00-	20	10	30	67	33
4.20-	8	4	13	62	31
4.40-	3	1	3	(100)	(33)
Ecclesall Beech-Chestnut-Oakwood					
3.20-	0	0	1	(0)	(0)
3.40-	7	7	12	58	58
3.60-	8	12	19	42	63
3.80-	19	16	30	63	53
4.00-	13	2	13	100	15
4.20-	5	0	5	(100)	(0)
4.40-	0	0	1	(0)	(0)

Note. Percentages which are misleading through being calculated from very few samples are bracketed.

Table 3. *pH values at which neither Holcus nor Deschampsia dominates the soil*

Wood	pH value x_0	Common % occurrence
Totley	3.65	68.1
Limb Brook	3.84	44.5
Ecclesall	3.72	55.9

3.2. Combined effect on distribution of acidity, moisture and organic contents

3.21. As a preliminary to the investigation of the combined effect of pH, percentage moisture and percentage organic content, on frequency of occurrence, their intercorrelations were calculated, and scatter diagrams (examples of which are shown in Figs. 4 and 5) were plotted. Some of the relations involving pH showed a departure from linearity which proved to be statistically significant but not sufficiently serious to justify rendering the subsequent analysis complicated by taking it into account. The correlations between the variables for all woods except Lady Canning's (for which paucity of data made further

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investigation of little value), together with their standard deviations and the number of quadrats included, are given in Table 4.

Table 4. *Intercorrelations of percentage moisture, percentage organic content, pH and occurrence index*

Wood	r_{yx_1}	r_{yx_2}	r_{yx_3}	$r_{x_2x_3}$	$r_{x_3x_1}$	$r_{x_1x_2}$	S_y	S_{x_1}	S_{x_2}	S_{x_3}	n
Totley	+0.022	+0.455	-0.282	-0.631	-0.599	+0.681	0.851	6.55	13.6	0.259	121
Limb Brook	-0.092	+0.281	-0.384	-0.571	-0.502	+0.569	0.928	9.70	14.3	0.263	94
Ecclesall	+0.035	+0.176	-0.382	-0.472	-0.588	+0.847	0.890	10.40	13.5	0.218	77

y = occurrence index, x_1 = percentage moisture, x_2 = percentage content, and x_3 = pH.

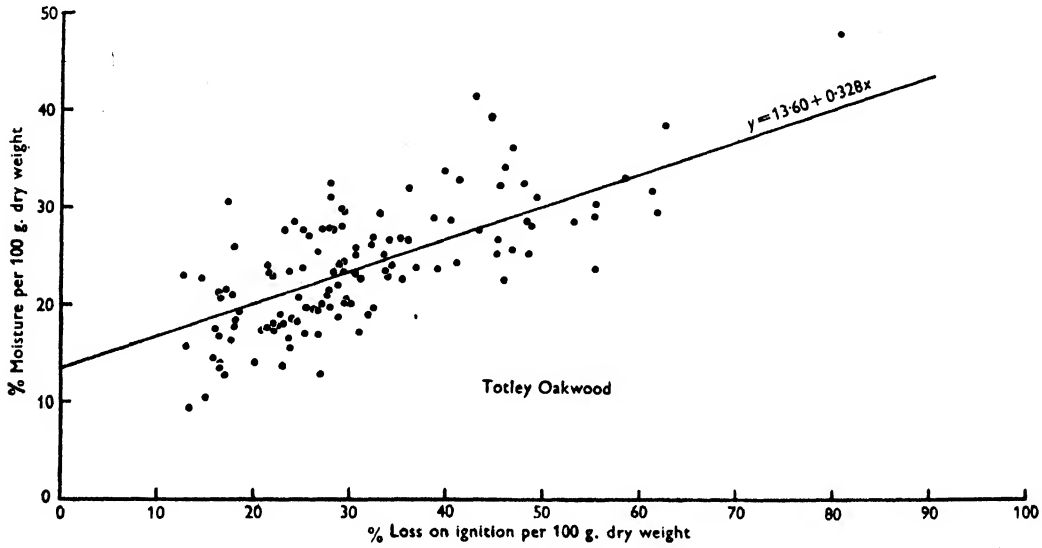


Fig. 4.

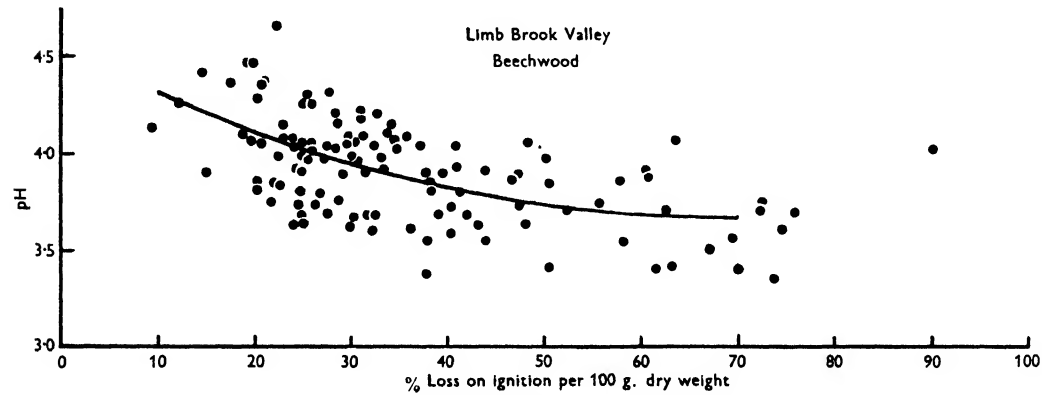


Fig. 5.

3.22. Each variable was also correlated with an occurrence index y defined as follows:
 $y = +1$, for quadrats bearing *Deschampsia* but not *Holcus*;
 $y = -1$, for quadrats bearing *Holcus* but not *Deschampsia*;
 $y = 0$, for quadrats bearing *Holcus* and *Deschampsia*.

These correlations, which are also given in Table 4, need some explanation. Assuming that the value of the occurrence index is an 'effect' and the other variables 'causes' of that effect (see § 1), then a value, say 0.3, of the correlation coefficient between the occurrence index and a variable will mean that the effect of an increase of one standard deviation in the variable is to increase the occurrence index 0.3 standard deviation. This interpretation will be used in § 3.26, but here a correlation will be simply regarded as a rough indication of the strength of the relationship between the two variables involved therein. For a fuller discussion, see Fisher (1944). *Note*: quadrats bearing neither species were excluded from the analysis, though the values relating thereto were plotted on the scatter diagrams.

3.23. From Table 4 the following conclusions may be drawn:

(a) There is a strong positive correlation between moisture and organic content or, in other words, high organic content implies high moisture content and vice versa.

(b) Both moisture and organic content are negatively correlated with pH; high pH implies low moisture and organic content, and vice versa.

(c) Percentage organic content is positively correlated, and pH negatively correlated, with the occurrence of *Deschampsia*; *Deschampsia* tends, in other words, to occur on soils having a high organic content and low pH. For *Holcus* the reverse is true.

(d) The small correlation between the occurrence index and the moisture percentage suggests that the latter has little influence in favouring one species at the expense of the other. The ecological implications of these conclusions will be discussed in § 4.2.

3.24. The strong correlations between the soil variables suggest further analysis in order to estimate what the effect of a change in each variable would be for samples so selected that the remaining variables were constant. Assuming, for instance, that we had a number of samples sufficiently large to enable us to select a sizeable group with percentage organic content and pH both constant (say near their mean values), then we would wish to know what change to expect in the occurrence of the two species with increasing moisture.

Such a selection cannot be carried out with the number of samples available, but a slightly modified form of the discriminant function of Fisher (1944) provided a useful substitute.

If we determine that function of the soil variables of the form

$$(a \times \text{percentage moisture}) - (b \times \text{percentage organic content}) - (c \times \text{pH}) - \text{constant},$$

which gives the most precise estimate of the occurrence index, it will have a value nearer -1 for samples where they tend to favour *Holcus*. A positive coefficient of a variable in this linear function—which may be regarded as an index of soil composition, or 'soil index'—shows that an increase in that variable, the other two remaining unchanged, will increase the function as a whole or, in other words, that the soil will become more favourable to *Deschampsia*. A negative coefficient implies a similar tendency towards *Holcus*. Thus, in a sense, the coefficient measures the 'effect' of the variable on the frequency of occurrence.

3.25. There are two useful forms in which the above function may be expressed: (a) the variables measured in terms of their original units when the values of the coefficients may be compared from one wood to another, equal values for the two woods implying an equal response of the species to changes in that variable in the two woods; and (b) the variables expressed in units of their standard deviations, when they are not easily compared from wood to wood (except in the improbable case of their standard deviations being the same in both woods), but are readily compared with the raw correlations in Table 4. In either

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case the coefficient gives the number of units of standard deviations by which the occurrence index is increased by an increase of one standard deviation in the variable; in the case of (a) with the other variables held constant and in (b) without this restriction.

The coefficients calculated on the basis of both methods are given in Tables 5a and 5b.

Table 5a. *Effects of an increase of one unit in percentage moisture, percentage organic content and pH on the occurrence index, the other two variables being held constant in each case*

Wood	% moisture	% organic content	pH
Totley	-0.0766	+0.0476	-0.515
Limb Brook	-0.0417	+0.0138	-1.585
Ecclesall	-0.0646	+0.0373	-2.350

Table 5b. *Effects of an increase of one unit of standard deviation in percentage moisture, percentage organic content and pH on the occurrence index (in units of standard deviations), the other two variables being held constant in each case*

Wood	% moisture	% organic content	pH
Totley	-0.58	+0.75	-0.16
Limb Brook	-0.44	+0.21	-0.44
Ecclesall	-0.78	+0.57	-0.57

3.26. It is at once evident from Table 5b that moisture has a determining effect on the frequency of occurrence of *Holcus* and *Deschampsia* spp.; a high moisture content is unfavourable to the occurrence of *Deschampsia* and favourable to that of *Holcus*, other things being equal. This effect is not revealed in Table 4, because, in general, high moisture is accompanied by high organic content and low pH, and the favourable effect of these cancels much of the adverse effect of high moisture on the occurrence of *Deschampsia*, for example. This cancelling effect is to a large extent true of the other relationships, a fact which is revealed in a general increase in the absolute size of the coefficients in Table 5b over the raw coefficients in Table 4.

3.27. From Table 5a it would seem that moisture and organic content have their greatest effect on frequency of occurrence in Totley wood, whilst the effect of pH is most marked in Ecclesall wood. Such comparisons can be variously interpreted in terms of height of water-table, geological type, uniformity and type of tree cover, and the like. Detailed comparison between the coefficients, however, cannot profitably be made at this stage, since the factors operating in the woods are insufficiently investigated.

3.28. An approximate indication of the extent to which the employment of the above technique has enabled us to give a more complete explanation of the presence or absence of the two species in quadrats in these woods is given by a comparison of the raw correlations of pH with the occurrence index in Table 4 with the correlations of soil index with the latter, as shown in Table 6 below.

Table 6. *Correlations of occurrence index with pH and soil index*

Wood	Correlation of occurrence index with	
	pH	Soil index
Totley	-0.28	+0.61
Limb Brook	-0.38	+0.41
Ecclesall	-0.38	+0.54

3.29. It must be noted here that in the simple treatment above the assumption has been made throughout that the frequency of occurrence of both species is a direct result of soil

conditions and not necessarily a cause of them. That *Deschampsia*, for example, may in fact affect the soil variables, probably in a direction favourable to *Holcus*, will appear in § 4 below. It must be noted too that we are dealing above with single determinations of factors which throughout the year may vary considerably, pH having been shown by Baker & Clapham (1939) to vary seasonally, for example.

4. ECOLOGICAL INTERPRETATION AND GENERALIZATION OF THE INVESTIGATION

4.1. From the values of x_0 given in Table 3, *Deschampsia*-dominated soils within the woodlands investigated usually appear to have a pH less than 3.75, and, similarly, *Holcus*-dominated soils a pH greater than 3.75. This result confirms the observation of Pearsall (1938*a, b*) that a pH of approximately 3.8 might be used as a dividing line between these two types. The results of Pearsall, however, were obtained from a consideration of the variation of pH values between soils from a variety of woodland types, and by use of the quinhydrone method of pH determination with a spade platinum electrode directly on undisturbed soil samples rather than the glass electrode on disturbed soil samples. That an analogous result is obtained despite this, and the use of a 2:1 water:soil ratio suggests a further investigation into the potential drifts observed by Pearsall, and possibly into the problem of the use of the quinhydrone method of pH determination on highly organic acid soils. Boswell (1948) has recently obtained results which appertain to this latter point.

4.2. Ecological observations indicate that, following the bryophytes and fungi, *Deschampsia flexuosa* is one of the first colonizers of raw woodland soils, being followed in many cases by *Holcus mollis*, etc.; also that *Deschampsia*, more especially in Coal Measure woodland, is often in adverse competition, to a greater or lesser extent, with *Holcus* (compare the observations of Watt (1931), of Woodhead (1906), and of Ovington (1947)). Thus it can be assumed, with some degree of certainty, that the present situation within these woodlands is to a large extent the result of the continuing overgrowth, to varying degrees, by *Holcus* of the *Deschampsia* areas.

Now it has been shown in § 3.26 that, other things being equal, *Deschampsia* appears to occur more frequently on the drier situations and *Holcus* on the moister situations; and further, that *Deschampsia* prefers a more highly organic soil of relatively low pH, as compared to *Holcus*. Hence, there is evidence of a progression in soil characteristics involving a decrease in organic content, an increase in moisture relative to organic content, and an increase in pH. Such a progression has two alternative explanations:

(a) the soil changes are effected directly and/or indirectly through the microflora, by *Holcus*, during and after overgrowth of the *Deschampsia* areas; or

(b) that *Deschampsia* may initiate a series of soil changes in a raw humus soil which are responsible, at least in part, for its overgrowth by *Holcus*. These changes may involve some or all of the effects above: for example, *Deschampsia* by providing a mass of fibrous roots and leaf bases, the latter usually in laminated layers, may increase surface moisture content by preventing free percolation of water. Other suggestions could be advanced, their overall effect being to produce conditions conducive to the advance of *Holcus*.

Both (a) and (b) may be true to some extent; what remains true is that the succession, raw humus soil → *Deschampsia*-dominated soil → *Holcus*-dominated soil, involves changes which represent a progression (or stage in the 'upgrade series' of Watt (1947*a*)) from an essentially mor type towards the mull type; and the change in moisture content implies a change from the more xerophytic vegetational type, with *Deschampsia* as representative,

to the more mesophytic, represented by *Holcus*. This conclusion agrees with that deduced from ecological results, and the appearance of many soil profiles confirms the opinion of P. E. Muller that *Deschampsia* may be used as an indicator of mor type soils, and supports the contention inherent in the results of Pearsall (1938a) that the relative extents of the *Holcus* and *Deschampsia* areas in such woodlands could be used to indicate the extent to which their soils have progressed from a mor towards a mull type. This may have interest from a silvicultural point of view, as instanced by Watt's observations (1923) on the regeneration of beech in the two types.

It may be noted here that Watt, in his account of the Scottish wind-belt beechwoods, attributes the primary effect of wind on the success of *Deschampsia* to litter removal. While this may be true, the drying effect may also have a considerable bearing on occurrence and success of both *Holcus* and *Deschampsia*.

4.3. Passing now to the prediction of the wider occurrence of these two species, we will deal first with *Deschampsia flexuosa*, then with *Holcus mollis*.

4.31. The soil preferences of *Deschampsia* have been outlined above—a soil of low pH, highly organic and dry. These last two characteristics being mutually incompatible, perhaps the best compromise will be found on exposed, steep slopes, with highly organic acid sandy soils such as often occur under woodlands of pine, birch and *Quercus sessiliflora*, more especially the first, and, less frequently, of beech. The alternative situation consistent with these demands is the open acid sandy soils of heaths, but as such open situations invariably involve *Deschampsia* in competition with other species, notably *Calluna*, *Pteridium* and *Vaccinium*, we would suggest a preference, as far as success is concerned, for pinewood. Other considerations support this, such as the provision of a litter at once acid, slow of decomposition, and easily penetrable by *Deschampsia*, and a light intensity (in natural woodland), apparently adequate, if not optimal, for vegetative growth at least, without the consequences of competition. Due regard must be had for climatic variation, chance of immigration, etc., but on the whole we may tentatively assume a distribution of *Deschampsia* to some extent coincident with that of *Pinus sylvestris*, and an altitudinal limit at least as high as that of the latter. (Wilson (1931) reports *Deschampsia* at 3550 ft. on Snowdon, 3768 ft. on Lochnagar, though it has been reported as high as 13,000 ft. on the granite cone of Mt. Kinabalu in British North Borneo (Gibbs, 1911); Wilson reports *Pinus sylvestris* on Ben-na-Bourd at 2220 ft. and probably above this elsewhere.)

We can predict *Deschampsia* too as a frequent constituent of heathland, and of most high altitude woodlands, other than pine, over grit or sandstone. This agrees fairly well with the known distribution of *Deschampsia*; perhaps the best examples are its occurrence in the well-known Ballochbuie and Rothiemurchus Forests of the Highlands (Tansl y, 1939), on Mendip, Quantock and Exmoor (Watson, 1932), on the Pentland and Moorfoot Hills (Smith, 1918; Wyllie-Fenton, 1940), in Hindhead, Oxshott and Esher Commons (Fritsch & Parker, 1913; Summerhayes, Cole & Williams, 1924; Summerhayes & Williams, 1926), in the subalpine birchwoods (*Betula nana*) of the Swedish, Norwegian and Russian Laplands (Gates, 1928; Polunin, 1936; Vahl, 1913; Simmonds, 1912), and the subalpine pinewoods of the west Caucasus (R bel, 1914). Its absence in Breckland, with other usually typical heath species, is still not satisfactorily explained (Jeffreys, 1918). It may be remarked here that the soils with which we have dealt above are all essentially podsollic and therefore, if this be regarded as an expression of the preferences outlined above, then the occurrence of *Deschampsia* on the Carboniferous Limestone of Haycop Tor in Derby-

shire (Report on B.E.S. Meeting, 1947), Carrowkeel in north-west Ireland (Webb, 1947), etc., where the soils show incipient podsolization, calls for small comment.

4.32. The preferences of *Holcus*, as the more mesophytic type, for soils of higher pH than those demanded by *Deschampsia* in those woodlands where they occur together, suggests an altitudinal limit for *Holcus* below that of the latter (Wilson records *Holcus* at 1900 ft. in west Lancashire, 1750 ft. in Atholl, Scotland), and probably coincident to some extent with the maximum altitude attained by woodlands on the Coal Measures, say less than 2500 ft. The presence of tree cover, or of *Pteridium*, is assumed to be essential for the occurrence of *Holcus* at such altitudes, especially in exposed situations, as a safeguard against excessive transpiration and desiccation of the soil. It is probable that *Deschampsia* may serve a similar purpose to some extent, as, indeed, may accumulated leaf litter, the latter more important probably in the early part of the year. As for its more general distribution in woodlands over sandstone, the indications are of a preference for the less steep, deciduous type, with soils essentially mull in character. Where the woodlands are steep, its location will be in the base accumulated, moister (which often imply litter accumulated) areas on the bottom slopes, or in similar depressions higher up the slope, and by the sides of streams and flushes. Undoubtedly, an increase of light intensity to full daylight would be beneficial, but as with *Deschampsia*, open situations usually involve intrusion of other species, notably *Pteridium*. With the latter, however, *Holcus* has one advantage over *Deschampsia* in that it forms, with *Scilla non-scripta*, the well-known complementary society *Scilla-Holcus-Pteridium*. The effect of species such as *Pteridium*, therefore, is to influence success rather than occurrence of *Holcus*. Overall, therefore, the best situation suggested for *H. mollis* appears to be in the relatively base-rich, well-drained, yet moist, sandy, mull type woodland, with a light intensity low enough to prevent development of *Pteridium*, while at the same time adequate for vegetative growth of *Holcus* at least. The Coal Measure woodlands, and such woodlands as occur on lowermost slopes of the Millstone Grit, suggest themselves. Sycamore, as providing a mull-type soil, etc., is suggested as the best tree type where it occurs in such woodlands: *Quercus sessiliflora*, with leaves opening late in spring, usually involves *Pteridium* intrusion, and *Fagus* too low a light intensity. Such a distribution is consistent with the known distribution of *Holcus*. We need only quote Woodhead (1906), Moss (1913), Watt (1931), Adamson's account of Gamlingay Wood (1912), and that of Salisbury on the oak-hornbeam woods of Hertfordshire (1918).

4.4. A particular value of pH in one locality may imply a very different nutrient availability from that implied by precisely the same value in a different locality. Hence, we advise the carrying out of careful statistical and ecological comparisons between the results of investigations in different areas before any attempt is made to combine them into one analysis (compare, for instance, Hora, 1947). Further, it is obviously impossible to separate any single factor from the physiological complex of factors governing any species, in the absence of information as to the remainder, and then attach the adjective 'optimum'; but even without this caveat, our own investigation has provided no evidence for a well-defined optimum pH value or range in any of the separate woods, since there is no evidence that any of the occurrence curves of § 3.17 is anything but monotonic. It is, in fact, difficult to envisage a situation where the whole of the probability curve $P(x)$ of § 3.12 can be fitted to homogeneous data from one locality, in view especially of the usually restricted range of pH where the substratum is geologically homogeneous. The difficulty

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does not arise with species such as *Deschampsia* growing in that pH range below which soils rarely occur in this country at least. It would be interesting to see if the curve could be obtained for a species of limited pH range, or perhaps for pasture species where the pH range of the soils may have been increased by irregular application of lime, etc. Alternatively, it might be possible to obtain a curve of this type using a soil index of the type derived above, as an argument instead of pH, though care would be needed in the interpretation of such a curve.

4.41. As far as collection of samples goes, we note Bayhard Hora takes the precaution of sampling the soils to a depth consistent with that where most roots of the species occur. We would recommend further a more randomized method of transect marking than that first adopted by us.

We wish to thank Prof. A. R. Clapham for his stimulating and oft-rendered criticism; Mr J. G. Boswell for his encouragement and advice, and the Parks Department of Sheffield Corporation for their co-operation in the above investigation.

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THE VEGETATION OF ST KILDA IN 1948

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(With two Maps in the Text)

AND AN APPENDIX: REPORT ON PEAT SAMPLES FROM ST KILDA

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1. INTRODUCTION

During July 1948, a party of eight biologists, under the leadership of Dr F. Fraser-Darling, spent a fortnight on the islands of the St Kilda group. The purpose of their visit was to record as far as possible changes in the fauna and flora since the Oxford and Cambridge party made the last survey in 1931. This paper is one of a series dealing with the ecological work of the expedition. To the zoologist these islands have always had a peculiar interest, especially centred upon the three endemic subspecies (the wren and the two mice), the Soay sheep and the multitude of nesting birds. The botanists' material is less striking. The flora bears a general resemblance to that of the Outer Hebrides and, indeed, of the west Highland mainland, although poorer in number of species. In fact, it was the opinion of Turrill (1927) that the moorland vegetation (representing the majority of the native species) was probably merely a detached piece of west Highland vegetation. Certainly

there seems to be no evidence of geographical subspeciation, perhaps because the environmental conditions differ too little from those on the west coast mainland.

A new and wide field of interest has, however, been opened by the evacuation on 26 August 1930, of the total then resident human population of forty-three and their grazing animals. The island has thus been allowed to revert to a wild state, and interaction between plants and animals can now take place without human interference. The Oxford and Cambridge expedition visited the islands in 1931 to make a record of the status of plants and animals at a time when the effects of human habitations were still potent. They forecast that considerable changes would occur in both plant and animal species. This forecast has proved correct.

The condition of the vegetation of a particular area at a particular time represents an equilibrium between all the factors acting on that vegetation. When one of these factors is removed the vegetation will adjust itself to a new equilibrium. The adjustment will occur at first by rapid change, and then progressively by slower alteration in which the residual effects of the factor are slowly, and often incompletely, effaced.

Both these phases are recognizable on St Kilda. It is unfortunate that no study of the vegetation has been possible in the interval 1931–48, for now the first phase of rapid change is almost complete and a more or less stable equilibrium has again been reached, which will probably only be subject to minor modifications in the future; unless, of course, some of the operative factors alter.

It was unfortunately impossible to visit any other islands but Hirta and Dùn. Time was too short and, although material was collected for a full survey of the vegetation, the facts are inadequate for presentation. It is intended therefore to discuss the vegetation from two points of view: the first relating to the changes which have occurred in the vegetation since 1931, showing that the vegetation has again reached a semi-stable condition, and the second to the influence of biotic factors on maritime grassland. Finally, as it seems desirable to keep the literature on St Kilda in a compact and readily accessible form, we shall include a few observations, which though not strictly relevant to the discussion, are yet of sufficient interest to merit being recorded.

Evidence for changes in the vegetation will be drawn from Petch's paper on the vegetation of St Kilda in 1931 (Petch, 1933).

Nomenclature is in accordance with the 'Check List of British Vascular Plants' (Clapham, 1946).

2. TOPOGRAPHY AND GEOLOGY

St Kilda is a group of islands and stacs situated near the edge of the continental shelf about 110 miles west of the Scottish mainland and about 45 miles west of the Outer Hebrides. Of the four islands, Hirta, Dùn, Soay and Boreray, only two were visited, Hirta and Dùn, and these alone will be described in detail.

Hirta is the largest island ($2\frac{1}{4} \times 1\frac{3}{4}$ miles; area 1575 acres). It is the only one that was permanently inhabited, at least in historical times. It consists of two valleys; that of Gleann Mhor draining north-west into the Glen Bay, and another, drained primarily by the Amhuinn Mhor, facing south-east. Here alone (in the village bay) does the land slope gently to the sea. There is a sandy beach in the bay, which is said to disappear in the winter and is backed by a storm beach of immense boulders. The sand is entirely mineral in origin and supports no vegetation.

The remainder of the coastline is one of magnificent cliffs. Those of Conachair in the north are over 1300 ft. These cliffs are often topped by steep and dangerous slopes of grass.

Inland the contours are smooth and rounded. To the west of Gleann Mhor and the Amhuinn Mhor there is a long ridge running north-west and south-east (the Cambir, Mullach Bi, Mullach Mhor and Ruaival), and to the east of the watershed there are, from west to east, the plateau of Mullach Mhor, and the peaks of Conachair and Oiseval (1396 and 948 ft. respectively). These three protect the village bay from the north and north-east.

Dùn is both topographically and geologically a part of the west coast ridge. The pro-

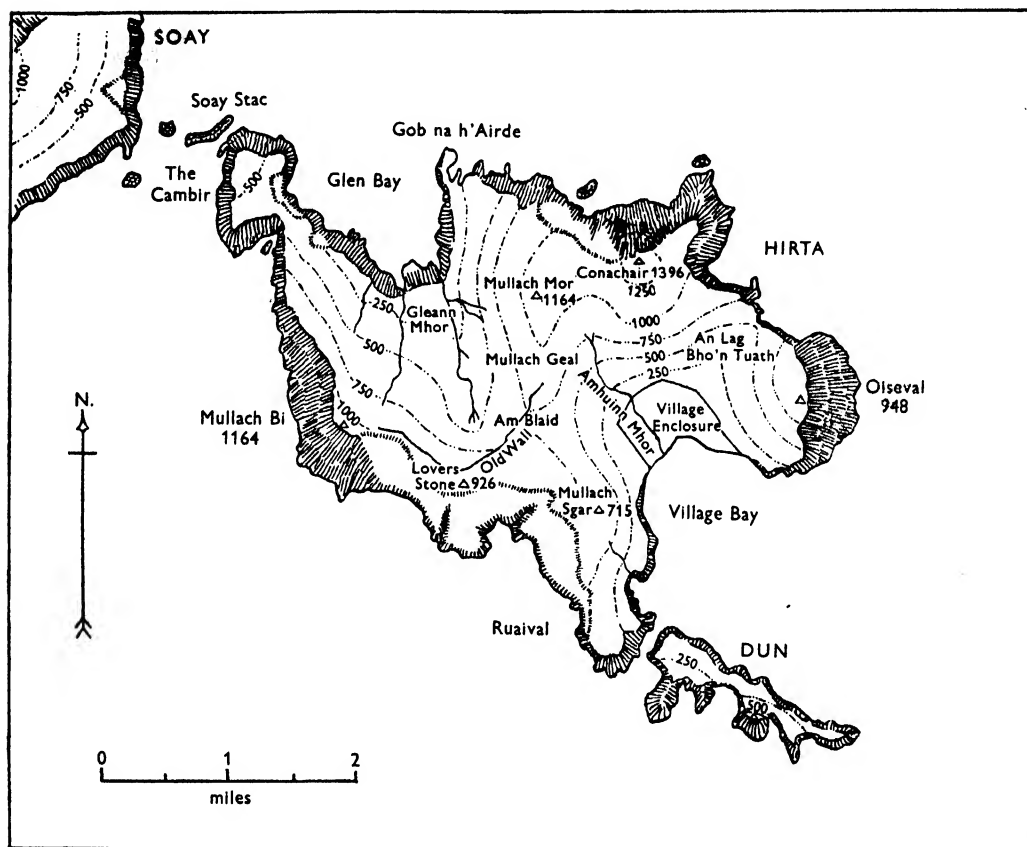


Fig. 1. Physiography of Hirta and Dùn, St Kilda.

cesses which have brought about its separation can be seen at work in the tunnels which pierce Gob na h'Airde and the narrow neck of Dùn itself. The strait that separates the two islands is only about 15 yards wide, but it is guarded on the Dùn side by a cliff about 100 ft. high, an impassable barrier to the passage of any land mammal. Dùn has a coastline of length 2 miles, and its area is 79 acres.

Geologically the group is an intrusive mass of igneous rocks, varying from acid granophyre, to a gabbro, olivine eucrite with a high base content (11.18% CaO; Cockburn, 1935). The west coast ridge is composed entirely of olivine eucrite, and the Conachair-Oiseval mass of granophyre. Mullach Mhor and the sides of Gleann Mhor, including part

of Mullach Sgar, are made up of gabbros and dolomite, with a medium base status. Cockburn (1935) was unable to find any conclusive evidence of glaciation.

3. CULTIVATION AND GRAZING

The village enclosure was the only part of Hirta to be cultivated, and this cultivation was of the lazy-bed type. The area under crops decreased steadily during this century, and had dwindled almost to nothing by 1930. The number of sheep too had dropped. The island once supported about 1300 black-faced sheep, but only 500–600 were left at the time of the evacuation, and these were all removed to the mainland. Therefore at the time of the 1931 expedition there were no grazing animals on Hirta at all, and there was promise of a fascinating ecological experiment. However, in 1931 the present owner introduced 107 of the native breed of sheep from Soay, and any regrets about this must give way to pleasure at the subsequent increase in the numbers of this unique beast.

On Dùn the state of affairs was quite different. There is evidence of a little former lazy-bed cultivation at the north-west end, but this has certainly not been tilled within the century. Small numbers of sheep were grazed on Dùn at least as late as 1909 and probably later, but there has been no grazing at all since 1930.

Finally, there was a summer shieling at the foot of Gleann Mhor. The households moved over to the shieling in June and left in September. The sheep would be caught every evening for the milking of the ewes, and the lambs were penned close at hand. Thus the ground around the shieling would receive more manuring and trampling than elsewhere.

To summarize: on Hirta the grazing factor was active until 1930, when it was totally removed. From 1932 to the present day it has again been gradually increasing. On Dùn the effect of grazing was never great and has been totally absent since 1930. Rabbits have never been introduced on St Kilda.

4. VEGETATION

There follows a review of the vegetational changes that have taken place in the last 17 years, and a survey of some of the more interesting ecological features. For this purpose it is convenient to consider the vegetation under four headings:

- A. Moorland.
- B. Formerly cultivated land.
- C. Maritime grassland.
- D. Zoophilethismic vegetation (vegetation altered by intense animal occupation).

A. MOORLAND

The moorland is complex in structure, and it proved impossible to analyse its complexity in a short visit. Petch (1933) gave a generalized account, and his description of the floristic composition of the communities still holds good. Their similarity to the heath-moorland communities of the west coast has already been mentioned. Many mainland species however are absent, e.g. *Rhynchospora alba*, *Eriophorum vaginatum* and *Carex dioica*, and others are unaccountably rare, e.g. *Scirpus pauciflorus*, *Drosera rotundifolia* and *Vaccinium vitis-idaea*. One plant of *Erica tetralix*, the first recorded, was found in 1931. There is still only one. It produces flowers but is straggling in growth and looks most unhealthy. Suitable habitats for these plants seem to be present in abundance. It would be interesting

to discover by breeding experiments whether in the small populations concerned races have arisen with specialized physiological requirements.

If one neglects small local changes in vegetation a broad distinction can be made between the granophyre block (Conachair and Oiseval), and the area of the more basic rocks including Mullach Sgar, Mullach Bi and Mullaich Mhor. On the former there is a tendency towards Calluneta and Ericeta, and on the latter towards Nardeta. All are subject to local variations. The vegetation of the summit plateaux shows some affinity to that of the mainland tops; there is an increase in the proportion of *Rhacomitrium*, and such species as *Lycopodium selago* and *Carex rigida* appear occasionally. Two *Eriophoreta angustifoliae*

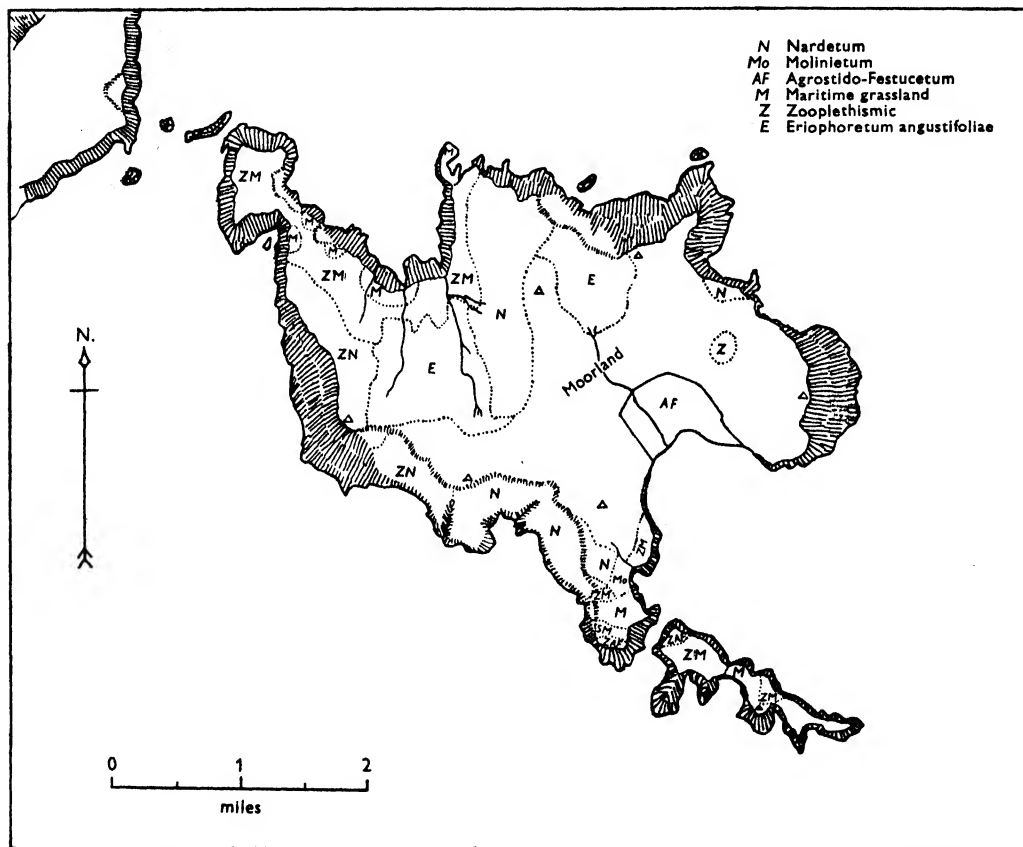


Fig. 2. Map of chief plant communities of Hirta and Dùn, St Kilda.

of large content occur, one stretching west from the summit of Conachair over the saddle between it and Mullach Mhor, and the other occupying the floor and part of the west side of Gleann Mhor. The latter shows a considerable admixture with *Empetrum* sp. There is a *Scirpetum* in a characteristic position at 700 ft. on the lip of the Amhuinn Mhor, and one north-east of the crags Glacan Conachair. *Molinieta* occur in the gullies of the inland cliffs, and one, which will be mentioned below, on the edge of the cliffs near the peninsula of Ruaival. The whole area was described in 1931 as dominated by *Festuca ovina* (certainly including *F. vivipara* if not entirely this species), and *Nardus stricta*. *Calluna vulgaris* and *Erica cinerea*, where present, were always grazed down to turf level, and were only apparent

on close inspection. This is no longer true. In the period during which the population of sheep was reduced the heather was able to reach a height of about 6–9 in. (and more in favourable localities). At this height it remains. The young growth is cropped, but the old and tough lower branches remain untouched. There is better grazing on the maritime grassland. In this state it is likely to remain. Fire would restore the 1931 condition (there are enough sheep to keep the heather down to turf level); but natural or even artificial fires are now most unlikely on Hirta.

Unfortunately, neither of the two permanent quadrats laid down in 1931 could be discovered, and so it was impossible to assess exactly and objectively how great the change had been. From general observation, however, it would seem that, although the balance of the dominants has altered, the frequency of the subordinate species is unchanged.

In addition to these changes there are a few points concerning individual species that are worth passing reference.

Luzula maxima. This species is confined on Hirta to the granophyre cliffs and the areas of moorland immediately adjoining them. It is dominant on the larger ledges of these cliffs (untenanted by sea birds), and has become dominant also on the summit of Conachair itself, associated with an heterogeneous collection of plants, which otherwise occur in moorland or cliff habitats. These are as follows: *Luzula maxima* and *Eriophorum angustifolium* (codominant), *Cerastium vulgatum*, *Deschampsia flexuosa*, *Potentilla erecta*, *Rumex acetosa*, *Agrostis stolonifera*, *Anthoxanthum odoratum*, *Scirpus caespitosus*, *Plantago lanceolata*, *Nardus stricta*, *Juncus squarrosus*, *Vaccinium myrtillus*.

Schoenus nigricans, of which two plants were found in 1931 on the plateau of An Lag Bho'n Tuath, is now several hundred strong. It favours an open habitat (where perhaps turfs have been cut), open patches of granophyre pebbles with a superfluity of running water, colonized sparsely with such plants as *Pinguicula vulgaris*, *Carex tumidicarpa*, *C. panicea*, *Ranunculus flammula*, *Narthecium ossifragum*, *Molinia caerulea*, *Scirpus caespitosus* and *Plantago maritima*.

Gentiana campestris. This species was reported as very rare in 1927 (Turrill, 1927); it was 'abundant everywhere' in 1931 (Petch, 1933). No plant could be found anywhere this year. It would be interesting to know if this change is part of a periodic fluctuation in numbers and whether the species is subject to these fluctuations elsewhere.

B. FORMERLY CULTIVATED LAND

(a) Grassland

The ex-cultivated land proved to be of greater interest than the moorland. In 1933 Petch noted that fields deserted for only 2 years resembled almost exactly those abandoned for many years. The same is true now. The area is covered by a more or less uniform grassland, but this differs widely from the grassland which was there 17 years ago. Then it was dominated by a rank growth of *Holcus lanatus*; now it is an *Agrostis-Festuca* grassland invaded by *Anthoxanthum*. *Agrostis* and *Anthoxanthum* are co-dominant, *Holcus* and *Festuca* abundant.

Lists for this area in 1931 are as follows:

Dominant: *Holcus lanatus*.

Abundant: *Ranunculus acris*, *Trifolium repens*, *Cerastium vulgatum*, *Agrostis tenuis*, *Anthoxanthum odoratum*, *Potentilla anserina*.

Frequent: *Angelica sylvestris*, *Luzula campestris*, *Rumex acetosa*, *Rumex obtusifolius*, *Plantago lanceolata*, *Lolium perenne*, *Poa trivialis*.

Occasional: *Leontodon autumnalis*, *Pteridium aquilinum*, *Euphrasia vulgaris*, *Festuca ovina*.

Rare: *Prunella vulgaris*, *Potentilla erecta*, *Senecio jacobaea*.

Locally frequent: *Vicia sepium*, *Achilles millefolium*.

Not all of these species are characteristic of the present *Agrostis-Festuca* grassland. The following list shows the present status (letters in brackets are 1931 frequencies):

<i>Agrostis tenuis</i>	c.d.	(a.)	<i>Leontodon autumnalis</i>	o.	(o.)
<i>Anthoxanthum odoratum</i>	c.d.	(a.)	<i>Luzula campestris</i> (agg.)	o.	(f.)
<i>Festuca</i> spp.	a.	(d.)	<i>Rumex acetosa</i>	o.	(f.)
<i>Ranunculus acris</i>	a.	(a.)	<i>Vicia sepium</i>	l.f.	(l.f.)
<i>Trifolium repens</i>	f.	(a.)	<i>Euphrasia</i> sp.	r.	(o.)
<i>Plantago lanceolata</i>	f.	(f.)	<i>Prunella vulgaris</i>	r.	(r.)
<i>Cerastium vulgatum</i>	f.	(a.)	<i>Potentilla erecta</i>	r.	(r.)
<i>Angelica sylvestris</i>	o.	(f.)	<i>Ranunculus ficaria</i>	r.	—
<i>Potentilla anserina</i>	o.	(a.)			

A comparison of these frequencies reveals, in addition to a change of dominant, a reduction in several plants, e.g. *Cerastium vulgatum*, *Angelica sylvestris* and *Trifolium repens*. These changes depend on subjective assessments of frequency by two independent observers, and too much weight must not be placed upon them. But they are consistent with the change of dominance. It would appear, therefore, that the state in 1931 represented one stage in the succession from abandoned cultivated land to the present closed grassland. *Holcus*, as a dominant, is characteristic of semi-open habitats (recently cut woodland for example), and tends to be replaced during the development of closed grassland. The other changes of frequency could also be accounted for on the same hypothesis.

The community probably is a stage of a plagiosere controlled by the grazing of sheep. It seems likely that if this influence were removed the area would slowly revert to moorland. In 1931 the area inside the enclosure and west of the Amhuinn Mhor was intermediate between ex-cultivated land and moorland, and now the area to the east of the Amhuinn Mhor also shows evidence of colonization by moorland species.

Pteridium aquilinum occurs in areas both above and below the village street. It is generally 6 in. to 1 ft. in height, but in sheltered localities it may be 2 ft. It seems to have increased since 1931, but only in extremely favourable localities protected from the wind (as, for example, small sheep enclosures) has it attained full dominance.

There is a small area of former lazy-bed cultivation on Dùn. This, although ungrazed, is similar in floristic composition to the village enclosure, and differs markedly from the rest of Dùn.

Festuca rubra, *Agrostis tenuis* (co-dominant); *Holcus lanatus*, *Rumex acetosa* (abundant); also *Potentilla anserina*, *Ranunculus acris*, *R. ficaria*, *Angelica sylvestris*.

(b) *Abandoned buildings and the area surrounding them*

Of the semicircle of slate-roofed houses and original 'black' houses that used to stand along the village street, only three now retain their roofs. The others are open to the weather and full of the decaying rubble of doors and furniture which provides shelter for a luxuriant growth of *Holcus lanatus*, *Angelica sylvestris*, *Lolium perenne*, *Poa trivialis*, *Stellaria media*, *Rumex acetosa*, *R. obtusifolius*.

All these plants occur in the general list of the 1931 survey for the village enclosure, but

they are now (in the enclosure, and excepting *Angelica* and *Holcus*) almost entirely confined to the near vicinity of the ruins and to the ground surrounding cleits. These latter are oblong stone buildings with turfed roofs built for the drying and storage of hay, fishing nets, bird carcasses, etc., and now much frequented by sheep for shelter, and also, to judge by the number of skeletons which were found inside, as a haven into which they retire before dying. The frequent trampling and manuring to which the ground round the cleits is subjected differentiates its flora from the surrounding grassland. In the village street and ruined houses and in the manse garden and on the gun-site remaining from the 1914-18 war, there occur also the remnants of those plants classified by Turrill (1927) as Introduced Plants. A full list of these follows, with notes as to their status in 1927, 1931 and 1948.

(c) *Introduced plants*

(1) *Weeds of cultivated ground*

Capsella bursa-pastoris. 1927: manse garden and near houses. 1931: present. 1948: absent.

Cardamine hirsuta. 1927: present. 1931: absent.

Spergula arvensis. 1927: a weed in the corn. 1931: absent.

Stellaria media. 1927: common on Hirta and growing in the corn. 1948: universally present in bird colonies, and around cleits in the village enclosure.

Chrysanthemum segetum. 1927: a common weed in the oats. 1931: present. 1948: absent.

Senecio vulgaris. 1927: in the manse garden. 1931: absent.

Galeopsis tetrahit. 1927: only as a weed in the corn. 1931: present. 1948: absent.

Plantago major. 1927: in the manse garden. 1931: present. 1948: common around the manse and in the manse garden.

Polygonum aviculare. 1927: manse garden. 1931: present. 1948: absent.

Agropyrum repens. 1927: Hirta. 1931: present. 1948: no specimens could be found after careful search.

(2) *Ruderals*

Potentilla anserina. 1927: in the manse garden and elsewhere between 20 and 100 ft. 1931: present. 1948: characteristic of formerly cultivated land and common around the manse, the factor's house and on Dùn lazy-beds.

Artemisia vulgaris. 1927: Hirta. 1931, 1948: absent.

Cirsium arvense. 1927: only outside the factor's house on a rubbish heap. 1931: present. 1948: in the same locality. It showed no evidence of flowering.

Cirsium lanceolatum. 1927: a few plants near the factor's house, the store and on Oiseval. 1931: present. 1948: common in the manse garden, but occurs also at the extreme south-west tip of the enclosed area, outside the factor's house and near the gun-site. It flowers freely and there are many flourishing seedlings.

Sonchus asper. 1927: sparingly on Oiseval cliffs, 200 ft. 1931: no record. 1948: one plant in a ruined house, one seedling in a heap of rubbish behind the village. The Oiseval locality was not checked.

Sonchus oleraceus. 1927: Hirta. 1931: present. 1948: absent.

Mysotis arvensis. 1927: on a little mound outside the factor's house. 1931: absent.

Rumex conglomeratus. 1927: near the houses. 1931: no record. 1948: present in the village enclosure.

Rumex crispus. 1927: near the houses. 1931: no record. 1948: Dùn; not seen on Hirta.

Rumex obtusifolius. 1927: near the houses. 1931: village enclosure. 1948: village enclosure.

Urtica dioica. 1927: only in the churchyard, about 150 ft., and in one spot near the sea-cliff at 40 ft. o.d. 1931: present. 1948: generally distributed in large patches in the churchyard and around the village street. It does not grow beside the cleits where nitrogenous manuring is high. The present localities may perhaps be the sites of old middens. No evidence is available on this point. It is possible that the absence of nettle near the cleits is associated with the effects of constant trampling upon the nettle rhizomes (see Bates, 1935, 1938).

(3) *Escapes from cultivation*

Brassica sp., *Trifolium pratense*, *Sambucus nigra* and *Hordeum vulgare* have all disappeared. *Lolium perenne* remains common around cleits and in the manse garden.

Finally, *Bellis perennis* (not included in Turrill's list) may be mentioned. In 1927 one clump was found at about 400 ft. on the sheltered south-west slope of Conachair. In 1931 there was no record and it was presumed extinct. In 1948 it has appeared in the manse garden and in front of the factor's house (in considerable numbers in the former locality). This may be a later introduction made by visitors or seeds may have been turned up and germinated since 1931.

(d) *Summary*

The vegetation of the village enclosure has reached a fairly stable condition controlled by grazing. The cultivated area has become a bent-fescue grassland of relatively uniform composition, with local variations due to manuring, the presence of bracken, and the occurrence of moisture-loving plants around springs.

Some introduced species have taken to natural or semi-natural habits. Of the others, the annuals and biennials have died out, some of the perennials persist. The disappearance of *Agropyron repens* is strange. It must, however, be remembered that it is impossible to prove that a plant has disappeared. Seeds may well remain dormant beneath the ground and merely await suitable conditions to germinate. It would be interesting to dig the surface of a small area and see what weeds still persist as seeds, or to bring back some soil for detailed examination.

It is possible that in the absence of disturbance puffins might take to nesting there, or the Atlantic seal might use it as a breeding ground, in which case profound and interesting modifications might be expected (cf. Darling on Rona; Darling, 1947).

C. MARITIME GRASSLAND (*PLANTAGO* SWARD)

A close study was made of those areas classified by Petch (1933) as moorland areas affected by sea-spray. They clearly fall under Tansley's category of Maritime and Sub-Maritime Grassland. The characteristic association is the *Plantago* sward described by Praeger (1911, 1934) from Clare Island, co. Mayo, and on other exposed western islands. On St Kilda, however, it is floristically poorer than the examples quoted. This association occurs on slopes up to an altitude of 600 ft., which may be drenched by spray in winter storms but are not exposed to direct wave action. Stages in its successional development were observed on eroded soil faces on Ruaival; and the mature association can be modified by the manuring and trampling of sheep, and the activities of birds.

The areas in question are the headlands of Ruaival and Gob na h'Airde, the lower regions of the west coast grasslands, and an area at the foot of Gleann Mhor. To these, listed by Petch, must be added the peninsula of the Cambir, and the island of Dùn. The latter, being ungrazed, was of particular interest as a control of the grazed association on the main island.

This vegetation was much favoured by the Soay sheep. Their headquarters were on the Cambir, and Ruaival was one of the main grazing grounds. As many as 200, over a quarter of the total estimated population, were observed on several occasions grazing on the latter. Between the two, and running the length of the west coast, there ran sheep paths, major thoroughfares, better marked by far than those on the moorland.

The account which follows was based on an examination of Ruaival, the Cambir, and the island of Dùn. The other areas were, however, visited, and nothing was found at any of them to invalidate the conclusions reached.

(a) *Boundaries*

The *Plantago* sward examined clothed the south-east slopes of Ruaival from an altitude of 140–500 ft. (This area also includes patches, which grew more extensive with altitude, of a vegetation, here termed Zooplethismic, which is considered to be derived from the *Plantago* sward by various animal agencies.) It is bounded on all sides but the north by cliff communities, and on the north by moorland. The transition zone is in general wide, but from 300 ft., down to near the cliff edge at 150 ft., the moorland is represented by a Molinietum, and the complete transition from *Plantago* sward to Molinietum occurs within a yard. A list of species noted on either side of the yard wide zone is appended. Their lack of correspondence is remarkable.

PLANTAGO SWARD:

**Festuca rubra*
Plantago maritima
P. coronopus
Leontodon autumnalis
Armeria maritima
Cerastium vulgatum
Sagina procumbens

MOLINIETUM:

Molinia coerulea
Anthoxanthum odoratum
Agrostis tenuis
Carex panicea
C. pulicaris
C. echinata
Festuca rubra
Holcus lanatus
Luzula multiflora
Nardus stricta
Narthecium ossifragum
Orchis ericetorum
Pedicularis sylvatica
Plantago lanceolata
Ranunculus acris
Sieglingia decumbens
Succisa pratensis
Viola riviniana

The Molinietum shows considerable resemblance to the Molinietum described from Uig (Wilmott & Campbell, 1945), and here seems to be a facies of the transition from *Plantago* sward to heath moorland conditioned by local differences of drainage or some other factor. It is almost certainly subject to drenching by sea-spray. It seems improbable that the distinction between the *Plantago* sward and Molinietum can be solely due to the grazing and salt-spray factors. Further and more detailed examination is necessary before definite conclusions can be drawn.

* Owing to the ban on collecting, very limited material was taken of this grass. This has proved inadequate for exact determination. The form of *Festuca rubra* occurring in Maritime Grassland is probably var. *pruinosa* Hack. det. C. B. Hubbard.

(b) Composition

The *Plantago* sward is founded on a substratum of deep peat (over 3 ft. on the Cambir). It consists in its purest form of a smooth green turf about 3 cm. in depth, composed of *Plantago maritima* and *Festuca* growing in intimate contact with one another as on a closely mown lawn. Rosettes of *Armeria maritima* occur at frequent intervals. Other species are almost totally absent. Evidence given in the Appendix suggests that the peat is actively formed by this community which can retain possession of the ground for long periods.

The composition of four quadrats (8 × 40 cm.) was examined in this pure association. (It was impossible to assess the area coverage, and the following figures give the number of 2 cm. squares in which the various species occurred.)

					Total
<i>Festuca</i>	76	74	61	—	211
<i>Plantago maritima</i>	69	54	40	58	221
<i>Leontodon autumnalis</i>	16	—	—	3	19
<i>Armeria maritima</i>	31	49	58	32	170
<i>Plantago coronopus</i>	—	—	—	17	17
<i>Cochlearia</i> sp.	—	—	—	1	1
<i>Cerastium vulgatum</i>	—	—	—	2	2
<i>Sagina procumbens</i>	—	—	—	6	6

(c) Possible succession

Above the strait between Hirta and Dùn there is an eroded slope partially recolonized by plants characteristic of the *Plantago* sward. This slope is set at an angle of 15–20° and is about 400 ft. high. Directly above the high-tide level there are about 50 ft. of rock, covered below with brown algae and almost devoid of vegetation. Then follows an unstable slope of soil and loose stones becoming progressively more stable at greater heights. This is suddenly succeeded by *Plantago* sward at an altitude of about 400 ft.

Two intermediate stages between bare ground and mature *Plantago* sward could be distinguished with numerous transition stages between them.

The movable scree was partially colonized by plants with long anchoring roots. This was an open community:

<i>Armeria maritima</i>	f.
<i>Plantago maritima</i>	o.
<i>P. coronopus</i>	o.

Part of the tap root was often exposed by the sliding away of surface soil. Isolated plants of *Festuca rubra* grew in hollows.

Higher up in small depressions where the angle was not so great the associations became nearly closed. The pattern of the first stage is still apparent, but the gaps are closed in by *Festuca*. The turf formed is not so homogeneous as the mature *Plantago* sward. Grazing seems to be a necessary condition for the production of the latter. Four quadrats were again examined here. Percentage coverage was estimated:

	%		%
<i>Festuca rubra</i>	54.25	<i>P. coronopus</i>	3.75
<i>Armeria maritima</i>	22.25	Unoccupied	1.75
<i>Plantago maritima</i>	20.00		

These stages represent a spatial succession to *Plantago* sward. This is probably also the course which a succession in time would normally follow. The typical *Plantago* sward is never actually achieved here. Erosion by various agencies, wind, wave action and puffs, destroy it faster than it can be regenerated by natural processes.

(d) *Maritime Grassland on Dùn*

The *Plantago* sward is confined on Dùn to north-facing slopes in the middle of the island. It is bounded below by cliff communities; above, it stretches to the crest of the ridge separating the north from the south side of the island, which is here very narrow; and at the sides it blends gradually into the zooplethismic vegetation. As would be expected it differs greatly from the grazed sward of Ruaival. The *Festuca* grows in a deep resilient turf (about 25 cm. from soil to leaf tips). Dry and withered leaves collect at the base of the shoots. *Plantago maritima* is restricted to a few large isolated plants with rosettes 10–15 cm. in diameter. The following species also occurred occasionally in the turf: *Leontodon autumnalis*, *Armeria maritima*, *Matricaria maritima* and *Cerastium vulgatum*.

This condition is closer to that of the second successional stage described above than to pure *Plantago* sward. It appears that *P. maritima* can only compete with *Festuca rubra* when the luxuriance of the latter is held in check by grazing or by adverse conditions.

The present condition of the *Plantago* sward on Hirta is strictly comparable with its state in 1931. The removal of the grazing factor had then not yet begun to have effect. The *Plantago* sward on Dùn was not examined in 1931.

D. ZOOPLETHISMIC VEGETATION

(a) *Hirta*

Scattered throughout the major plant communities on St Kilda (heath-moorland, *Agrostido-Festucetum* and *Plantago* sward) there are areas where occur, mixed with the other vegetation and sometimes entirely replacing it, species which appear to owe their presence to nitrogenous or phosphatic manuring and correlated disturbance by animals. Species, listed by Turrill (1927) as characteristic of such modified vegetation, are the following: *Ranunculus repens*, **Cerastium tetrandrum*, *C. vulgatum*, *Sagina procumbens*, *Trifolium repens*, *Achillea millefolium*, **Bellis perennis*, *Leontodon autumnalis*, **Senecio jacobaea*, *Prunella vulgaris*, *Plantago lanceolata*, *Rumex acetosa*, *Holcus lanatus*, *Poa annua*, *P. pratensis*, *P. trivialis*, **Arrhenatherum elatius*. (Of these the species marked with an asterisk are relatively uncommon and do not enter into the discussion.)

Modified vegetation has already been described from within the village enclosure. On the moorland the best examples were on the plateau of An Lag Bho'n Tuath. Here there are several stone enclosures inside which sheep used to be penned and even now congregate to graze. In and around the lower of these enclosures the following species were noted: *Anthoxanthum odoratum*, *Agrostis canina*, *Rumex acetosa*, *Holcus lanatus*, *Ranunculus acris*, *Juncus effusus*, *Stellaria media*.

In the upper enclosures the same species were found, but outside the prevalent species were those typical of the moorland, viz.: *Calluna vulgaris*, *Deschampsia flexuosa*, *Festuca vivipara*, *Potentilla erecta*, *Galium saxatile*, *Orchis ericetorum*, *Hypericum pulchrum*, *Nardus stricta*, *Holcus lanatus*, *Anthoxanthum odoratum*, *Scabiosa succisa*, *Euphrasia vulgaris* agg., *Viola riviniana*.

The area of the plateau was in 1931 covered with vegetation similar to that of the once cultivated land, viz. *Holcetum*.

At the bottom of Gleann Mhor in the neighbourhood of the summer shielings the transition from Moorland to Maritime Grassland is quite obscured by the abundance of these zooplethismic species.

It was with reference to the modification of Maritime Grassland that the closest study was made. Here both the change and the factors considered to be responsible were most easily assessed.

In two small areas on Ruaival in the midst of pure *Plantago* sward herring gulls and greater black-backed gulls were seen to congregate, and the presence of feathers and excreta suggested that these spots were regularly visited. Here, largely replacing the species of the *Plantago* sward, there grew the following: *Ranunculus acris*, *Holcus lanatus*, *Rumex acetosa*, *Trifolium repens*, *Leontodon autumnalis*.

This flora increased in frequency with altitude on Ruaival, apparently because the ground became more broken, and the hollows so formed were much frequented by Soay sheep. The summit of Ruaival was covered with bent-fescue grassland also much modified. An interesting addition to the flora in this locality was a *Poa*, infected with Nematode worms and hence pathological, but which has been provisionally determined as *P. irrigata*.

This flora is undoubtedly similar in nature, though different in detail to the 'lair flora' described by McLean (1945) from Worm's Head, south Wales. The term 'lair flora' has been avoided here because the modifying factor here is as often birds as sheep.

(b) Dùn

Before giving an account of the modified vegetation of Dùn, it will be well to attempt to describe the island itself. Not to do so would be to remove the vegetation from its context. For the island is unique. It is a long narrow ridge with a sharp crest, flanked to the south by cliffs from 300 to 500 ft. high, and to the north by steeply shelving slopes, broken here and there by outcrops of rock, and at the bottom shelving suddenly into the sea. These slopes are so riddled by puffin burrows that it is impossible to walk more than a few steps without raising a protesting groan from the inmate of some burrow, whose roof has been broken in. Dùn, with its 79 acres, is one of the biggest puffineries on St Kilda, and the population of the group is considered to extend to millions. When the puffins have been disturbed the air is full of clouds of birds whirling out to sea and back.

The vegetation is correspondingly remarkable. What areas are not covered by cliff communities and Festucetum support a luxurious growth of *Rumex acetosa*, which thrives on the unstable ground of the puffin colonies. The *Rumex* reaches a height of 2-3 ft., with a rank growth and foliage liberally spattered with bird guano. The soil is a deep damp peat, which must be greatly enriched by nitrogenous matter and by calcium and phosphates from fish bones. Associated species are: *Agrostis tenuis*, *Stellaria media*, *Holcus lanatus*, *Matricaria maritima* and *Angelica sylvestris*. All are of very robust growth.

It is notable that the characteristically nitrogen-loving species, *Urtica dioica* is absent. *Matricaria maritima* seems to be able to stand a greater proportion of bird guano than any of the other plants, and survives when all other components of the vegetation have been killed.

Petch in his description of puffin colony vegetation on St Kilda, gives the following composition on Dùn:

<i>Holcus mollis</i> (sic)	d.	<i>Festuca ovina</i> (sic)	f.
<i>Poa annua</i>	a.	<i>Ranunculus acris</i>	f.
<i>Stellaria media</i>	a.	<i>Potentilla anserina</i>	f.
<i>Rumex acetosa</i>	a.	<i>Angelica sylvestris</i>	o.
<i>Cerastium vulgatum</i>	f.	<i>Montia fontana</i>	r.

Of these *Potentilla anserina* is now almost confined to the area of old lazy-beds, and *Montia fontana* to wet springs. With the addition of *Matricaria* and *Agrostis tenuis*,

however, this list is the same as that made this year. But as in the formerly cultivated land there has been a change in the dominant, *Rumex acetosa* has replaced *Holcus lanatus*. This may perhaps be explained if it is assumed that the influence of earlier grazing still persisted in 1931 but has now totally disappeared.

(c) *Puffin vegetation*

Three different types of site were chosen by puffins for their burrows on Hirta and Dùn, ledges on the steep slopes surmounting the cliffs, holes in boulder scree, and open and sloping grassland.

The first were not examined in detail; the second showed a characteristic vegetation of *Stellaria media*, and the third produced very great changes in the surrounding vegetation.

On Mullach Bi below the Lover's Stone the burrows were surrounded by zoophilethismic vegetation, modified probably by the activities of the puffins themselves. There was some evidence that the plants were being killed by the puffins and were again regenerated when the puffins left. Regenerated vegetation was of the modified type, e.g. *Holcus*, *Leontodon*, *Agrostis*, etc.

A much clearer picture was, however, presented by the puffin colonies on Dùn. Here the vegetation was of two types, Festucetum and Rumicetum. Puffins did not in general burrow in the former, except near the ridge where the depth of turf was not so great. In places here the *Festuca* had been killed, and the burrows were then vacated by the puffins. The Rumicetum was riddled with puffin burrows, and did not seem to be in any way adversely affected.

It appears that one of two alternatives can happen where the *Festuca* has been killed. Either it and some of the soil underneath may be eroded away, or it may be regenerated. If the first is the case, the Rumicetum may represent a recolonization of ground left bare by erosion.

5. DISCUSSION

From these changes in vegetation (collected in tabulated form in Table 1), a scheme may be built up showing the convergence under intensive animal occupation of the three main soil-vegetation units, Heath-Moorland, Maritime Grassland and Agrostido-Festucetum.

The presence of pollen of *Pinus*, *Betula* and *Alnus* (see Appendix) provides strong presumptive evidence that at one time the islands supported woodland. The possibility of long-distance transport from the eastern mainland, though perhaps not to be entirely discounted, is made less likely by the strong and generally prevalent westerly winds.

It is evident that if such woodland existed it was largely replaced by moorland; though whether this was due to a climatic change at the opening of the sub-Atlantic period we do not know. Suitable sites in the moorland area doubtless retained relict woodland species, and in others arctic-alpine species survived. The maritime cliff communities have probably long been present, but Maritime Grassland may have been derived from moorland by the incidence of sea-spray, and from *Agrostis-Festuca* grassland by edaphic factors, exposure, and grazing.

In addition to causing modifications by his grazing animals, man tilled the land, and in so doing introduced both crop plants and numerous weeds of cultivation. Some of these depended for their existence on the continuance of cultivation; others found for themselves other niches where the ground was disturbed by sheep or birds. (Such in

particular are *Stellaria media* and *Poa annua*, which are here always associated with colonies of nesting birds.)

Table 1

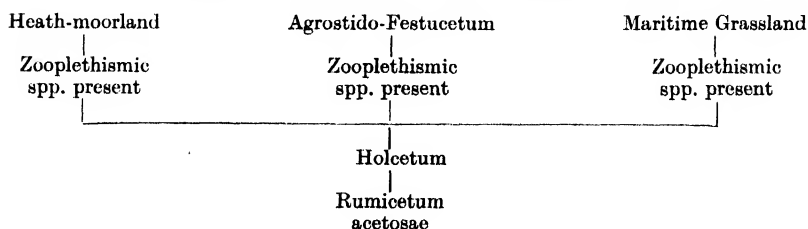
Place	Change in vegetation		Factors presumed to cause change
	From	To	
Am Lag Bho'n Tuath, Cambir	Moorland	Holcetum (1931)	Trampling and manuring followed by absence of grazing for one year Resumption of grazing
	Holcetum (1931)	Modified vegetation (1948)	
Cultivated land	Cultivated ground (Potato, <i>Hordeum vulgare</i>) (1927)	Holcetum (1931)	Abandonment of cultivation. Absence of grazing
	Holcetum (1931)	<i>Agrostis-Festuca</i> grassland (1948)	
Cultivated land and summit of Ruaival	<i>Agrostis-Festuca</i> grassland	Modified vegetation	Lessening of after effects of cultiva- tion. Resumption of grazing
Ruaival and Dùn	Maritime Grassland (<i>Plantago</i> sward)	Maritime Grassland (<i>Festucetum rubrae</i>)	Manuring and disturbance
Ruaival and Cambir	<i>Plantago</i> sward	Modified vegetation	Absence of grazing
Ruaival and Dùn	Modified <i>Plantago</i> sward	Holcetum	Grazing and disturbance
Dùn	Holcetum (1931)	Rumicetum acetosae (1948)	Grazing slight; manuring heavy. Burrowing on Dùn
			Heavy manuring; no grazing (? incidence of sea-spray). Bur- rowing

Table 1 implies:

(1) That a modified vegetation may be derived from Moorland, Maritime Grassland or *Agrostido-Festucetum* by manuring or disturbance.

(2) That this modified vegetation occurs in three different forms. In the first, subject to much grazing the original vegetation is invaded by certain characteristic species, *Holcus lanatus*, *Rumex acetosa*, *Cerastium vulgatum*, etc. In the second where grazing is diminished *Holcus* becomes dominant. In the third with no grazing, *Rumex acetosa* is dominant. The last may be dependent on the presence of sea-spray, but this is doubtful. *R. acetosa* is also abundant in small cracks on the north face of Conachair.

(3) That modified habitats in the village enclosure provide a suitable habitat for certain species that would otherwise die out.

Table 2. *Convergence of communities under intensive animal occupation*

6. SUMMARY

An account has been given of certain aspects of the vegetation of St Kilda. In particular, the changes which have taken place in the last 17 years have been studied. These are mainly due to the evacuation of the human inhabitants and to variation in other biotic factors. The three primary communities, heath-moorland, and *Agrostis-Festuca* and

Maritime Grasslands may all show modifications due to disturbance and manuring. Various states of this modified vegetation are described and a possible relationship between them deduced. An interesting field is open for study in the relationships between puffins and vegetation.

It seems desirable that a periodic record of the state of the vegetation should be kept. For this purpose a vegetation map (as detailed as time would permit) was prepared and numerous notes collected which are not included in this paper. They will be available to any botanist who wishes to make further study of this most interesting group of islands.

Finally, I should like to thank Dr H. Godwin for his great assistance in preparing the paper.

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APPENDIX

Report on peat samples from St Kilda

Three pollen samples, I, II and III, were taken respectively at depths of 1, 2 and 3 ft. from the surface at a site on the north-west corner of Hirta, on the sloping plateau surface at an altitude of approximately 400 ft. o.d., and in the community described by the author as *Plantago* sward. The base of the peat was unfortunately not reached. The results of pollen analysis of the samples are given in Table 3.

Many features of great interest emerge.

(1) Tree pollen is present only in very small frequency in comparison with the herbaceous pollen. It is about 5% of the total pollen catch in sample II, which, considering the extreme westerly position of St Kilda and the likelihood that prevalent winds would oppose carriage from the mainland, might be taken as an indication of the former presence of trees on the island, a conclusion supported by the discovery of small wood by Mr Poore.

(2) The presence of pollen of *Alnus* indicates a post-Boreal age for the peat.

(3) The virtual absence of *Sphagnum* spores, *Calluna* pollen or similar remains rules out the possibility that this is an old acidic moss peat modified subsequently by biotic factors, nor are the sedge-pollen percentages such as suggest a modified sedge-peat.

On the other hand, the enormous concentration of *Plantago* pollen suggests that peat may have formed from vegetation not unlike that now occupying the surface. The investigations of Iversen have pointed to the practicability of distinguishing between the Danish (i.e. British) species. In sample I this distinction has been made, and it seems certain that *Plantago maritima*, *P. lanceolata* and *P. major* (or *media*) are certainly present, although a large number of grains are crushed and not exactly identifiable. *P. maritima* grows locally dominant in the sward. *P. lanceolata* occurs abundantly when the animal influence is large,

Table 3

St Kilda	I (1 ft.)		II (2 ft.)		III (3 ft.)	
	Total	%	Total	%	Total	%
<i>Betula</i>	.	.	6	3	8	0.8
<i>Pinus</i>	.	+	1	0.5	1	0.1
<i>Alnus</i>	.	.	3	1.5	3	0.3
<i>Corylus</i>	.	.	6	3	2	0.2
<i>Salix</i>	1	0.1
Caryophyllaceae	5	1.3	14	7	3	0.3
Compositae-Matricaria type	+	.	2	1	.	.
Compositae-Taraxacum type	23	6	46	23	72	8
Cruciferae	+	.
Cyperaceae	.	.	4	2	.	.
Gramineae	15	4	58	29	9	0.9
Umbelliferae	1	0.3	2	1	7	0.7
<i>Armeria</i>	3	0.8	5	2.5	10	1
<i>Atriplex</i>	.	.	+	.	6	0.6
<i>Calluna</i>	+	.	1	0.5	.	.
<i>Callitha</i>	.	.	+	.	.	.
<i>Chenopodium</i>	+	.
<i>Montia</i>	4	1	4	.2	2	0.2
<i>Plantago maritima</i>	21	5
<i>P. major</i> or <i>media</i>	91	24
<i>P. lanceolata</i>	107	28
<i>P. coronopus</i>	+
<i>Plantago</i> undetermined species	100	26	43	21	846	88
<i>Ranunculus</i>	+	.	6	3	.	.
<i>Scabiosa</i>	+	.	+	.	.	.
Cf. <i>Ulmaria</i>	1	0.3
<i>Vaccinium</i>	.	.	+	.	.	.
Totals	371		201		970	
<i>Botrychium</i>	.	.	+	.	.	.
Filicales (naked spores)	.	.	1	.	.	.
<i>Ophioglossum</i>
<i>Polypodium</i>	+	.
<i>Pteridium</i>	+
<i>Selaginella</i>	+
<i>Sphagnum?</i>	+	.

(Analyses by Miss R. Andrew)

and *P. major* is present locally on the island though not in this region. *P. media* is not now recorded as living on the island. *P. coronopus*, which is represented by several grains, occurs abundantly in the *Plantago* sward. In samples II and III the labour of separating the *Plantago* species was not undertaken.

(4) After *Plantago* the next most abundant pollen is that of a composite type which might be *Taraxacum* or *Leontodon*, both of which are still present, the latter abundant as *L. autumnalis* in the turf hereabouts.

(5) There is a pronounced halophilous element in the herbaceous pollen, represented by grains of *Armeria*, *Atriplex*, *Chenopodium*, and perhaps by *Silene maritima* in the group Caryophyllaceae. The cruciferous type pollen may possibly also be of *Crambe maritima*.

(6) The *Armeria* pollen includes grains of three types, such as Baker has described for the dimorphic *Armeria vulgaris*: it is therefore presumably to this dimorphic aggregate that the island *Armeria* belongs.

(7) *Montia* pollen is not unexpected, since *Montia* grows freely beside springs on the island and Petch has recorded it from puffin colonies on Dùn. Similarly, the sparse spores

of *Polypodium*, *Pteridium*, *Botrychium* and *Selaginella* represent plants still living in the islands. *Ophioglossum* is, however, unrecorded. The genera *Scabiosa*, *Ranunculus* and *Vaccinium* are represented in the living flora of the island, but *Caltha* and *Ulmaria* (a tentative identification only) are apparently not.

It is evident that more thorough study of the island peat deposits could throw light upon its former flora and past vegetational changes; already this unpremeditated and short analysis seems to give evidence that a peculiar maritime type of peat may arise from *Plantago* sward, or related communities. This suggests inquiry into the nature of similar maritime peats, such, for instance, as are found on the Faroe Islands.

THE EFFECTS OF GRAZING ON THE BALANCE BETWEEN *ERICA CINEREA* L. AND *CALLUNA VULGARIS* (L.) HULL. IN UPLAND HEATH, AND THEIR MORPHOLOGICAL RESPONSES*

By C. H. GIMINGHAM, *Department of Botany, University of Aberdeen*

(With Plates 2-5 and four Text-figures)

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I. INTRODUCTION

The structure of many plant communities is much modified by biotic factors. The exact nature of their influence, however, is not always well understood, and the object of the experiments described here was to analyse in detail one example of their operation. Since the structure of communities is characterized more by dominant species than by any other single feature, attention has been concentrated primarily on the effects of grazing upon the dominants. Sheep-grazing provides a biotic factor susceptible of experimental treatment, and, in its relation to the maintenance or improvement of heather grazings, it is of considerable agricultural interest and importance.

The vegetation of a large part of the hill grazings in north-east Scotland belongs to the type known as 'upland heath', in which dominance is exerted either by *Erica cinerea* or by *Calluna vulgaris*, or frequently by the two species together as codominants. Their life-forms are closely similar, but their ranges of habitat tolerance, although widely overlapping, are not identical. Consequently, when occurring together, a delicate balance is established which is readily altered by an external factor. Such a community, therefore, is a sensitive index of the influence of a biotic factor.

* This paper formed part of a Thesis accepted for the degree of Ph.D. by the University of Aberdeen.

Communities dominated by *Erica cinerea* are normally found in drier situations than pure *Calluneta*, and frequently occur as stages in the subseral regeneration of *Callunetum* after burning. In such a subsera there is a period in which *Erica* and *Calluna* may be codominant, and it is the effect of grazing at this stage which has been investigated in particular. The results of a field experiment have been followed up by laboratory studies on the morphological responses to grazing in the two species. Data from these provide an interpretation of the field results, which is in agreement with evidence obtained from morphological analysis of material from the field.

II. FIELD EXPERIMENT

By arrangement with the Advisory Officer in Grassland Management of the North of Scotland College of Agriculture, observations were made during 1946 and 1947 on a field experiment laid out at Glensauigh, a hill farm situated 3 miles from Fettercairn in the county of Kincardineshire. The vegetation of much of this farm is typical of the upland heath community described by R. Smith (1900), W. G. Smith (1902, 1911), Elgee (1912, 1914) and Watson (1932) as that developed on shallow peaty humus overlying sandy or gravelly subsoils, in contrast to 'heather moor' on deeper peats. The experiment was designed by the Advisory Officer to study the general effects of various intensities of sheep-grazing on the regeneration of *Callunetum* following severe burning, and during the course of the experiment opportunity was taken to make a careful examination of the responses of the two dominant species, *Erica cinerea* and *Calluna vulgaris*.

(a) *Climate, physiography and soil*

(i) *Climate*

Glensauigh is situated in the foothills of the Grampian range, approximately 10 miles from the sea. It lies, therefore, in the climatic region of the north-east coasts, although receiving no direct maritime influence. No temperature records are available from the area in which the experiment was located, but figures from Montrose, situated on the coast 12 miles south of Glensauigh, indicate a relatively gentle fluctuation without severe extremes (averages over the periods 1916–20 and 1926–35 are given by the Meteorological Office as follows: mean for year 46·5° F. (8·1° C.); mean daily maximum 52·4° F. (11·3° C.); mean daily minimum 40·7° F. (4·8° C.)). Winter minima are, however, likely to be significantly lower at an altitude of 700 ft. (213 m.) above sea-level in the Grampian foothills, 10 miles inland.

Rainfall data are available from Fettercairn, 3 miles from the experimental area, and are given in Table 1, from which it appears that precipitation, although not high, is fairly evenly distributed throughout the year.

Table 1. *Rainfall means: Fettercairn, 1881–1915 (Meteorological Office)*

	J.	F.	M.	A.	M.	J.	J.	A.	S.	O.	N.	D.	Year
Inches	2·53	2·53	2·86	2·16	2·29	1·92	2·87	3·32	2·43	3·31	3·24	3·56	33·02

(ii) *Physiography*

Glensauigh is situated directly on the north highland fault. To the south of the fault line lies Strathfinella Hill, reaching 1097 ft. (334 m.) above sea-level, separated from the main highland massif by the valley of the fault line. The experiment was located on the north-

west aspect of Strathfinella Hill between the altitudes of 650 ft. (198 m.) and 775 ft. (236 m.), midway between the summit and a burn in the valley at 400 ft. (122 m.).

The experimental area extended to 6 acres, divided into twelve $\frac{1}{2}$ -acre plots (Fig. 1), and the following values for angle of slope (obtained with an Abney level at regular intervals from east to west across the area) indicate a steep slope with a slightly increasing angle towards the west: 16° , $17^\circ 30'$, $18^\circ 30'$, $19^\circ 30'$, 21° , $21^\circ 30'$.

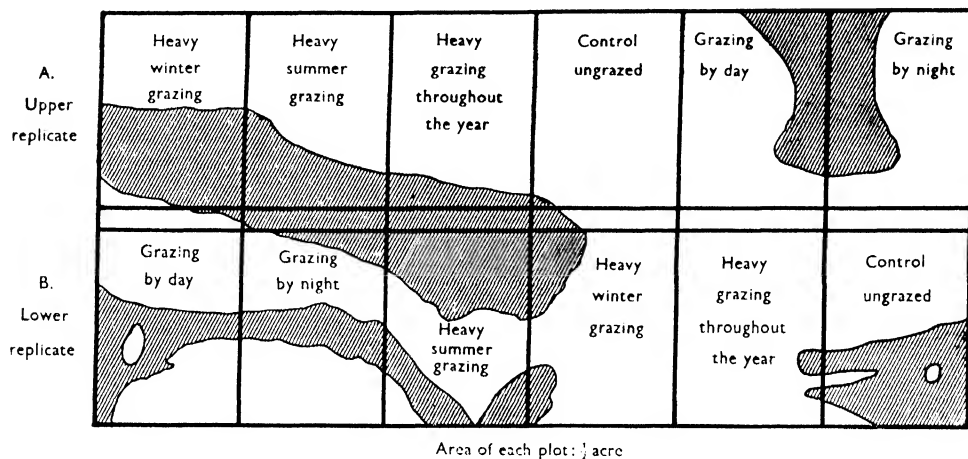


Fig. 1. Plan of grazing experiment: Glensauagh. Shaded regions less severely burned than the rest.

(iii) Soil

Strathfinella Hill has a rounded summit which has been heavily glaciated, and is composed of coarse conglomerates and sandstones of the Old Red Sandstone formation, in contrast to the schists north of the fault line. Much volcanic material is associated with the conglomerate in parts, but the higher ground of Strathfinella Hill is composed of a conglomerate containing pebbles of quartzite, schistose and granitic rocks.

A fairly deep glacial drift covers all the lower slopes up to about 700 ft. (213 m.), thinning out to a much shallower, pebbly and sandy drift at higher levels. The experiment was situated in the region in which the drift thins out, where only about 3 in. of material overlies it, so that any small excavations expose the reddish sandy and pebbly subsoil. The upper inch is a fibrous turf composed of the remains of *Calluna vulgaris* and *Erica cinerea*, while the lower 2 in. consist of a dark, more decomposed humus. The surface is strewn with granitic pebbles.

The following data, kindly supplied by the Macaulay Institute for Soil Research, are the results of analyses of bulked samples of the top 8 in. (20 cm.) of soil, taken from the hillside on which the experiment was located:

pH	4.9
Organic matter	11% (approx.)
Lime content	28 mg. CaO per 100 g.
Magnesium content	9.0 mg. MgO per 100 g. (approx.)
Phosphate content	< 1.0 mg. P_2O_5 per 100 g.
Potash content	15.2 mg. K_2O per 100 g.

The upper layers, therefore, have a composition characteristic of soils on which upland

heaths develop, low in lime content and acid in reaction, with an adequate potash content but very deficient in phosphates.

(b) *General vegetation*

At the particular stage of the burn subserotum at which the investigation was carried out the vegetation had the following composition (species listed approximately in order of frequency):

Dominant:	Rare (only a few individuals in the experimental area):
<i>Erica cinerea</i>	<i>Orchis mascula</i>
<i>Calluna vulgaris</i>	<i>Ulex europaeus</i>
Abundant (present in all experimental plots; percentage absence from $\frac{1}{10}$ sq.m. samples not greater than 75):	<i>Genista anglica</i>
<i>Carex pilulifera</i>	<i>Hypericum</i> sp. (seedlings)
<i>Deschampsia flexuosa</i>	<i>Chamaenerion (Epilobium) angustifolium</i>
<i>Agrostis canina</i>	<i>Anthoxanthum odoratum</i>
<i>Luzula multiflora</i>	<i>Sorbus aucuparia</i>
Frequent (present in all plots; percentage absence from $\frac{1}{10}$ sq.m. samples 75-95):	<i>Acer pseudo-platanus</i> } (seedlings)
<i>Vaccinium myrtillus</i>	<i>Robus fruticosus</i> (agg.) }
<i>V. vitis-idaea</i>	Bryophyta (in alphabetical order):
<i>Polygala vulgaris</i>	Musci:
<i>Galium saxatile</i>	<i>Bryum ?atropurpureum</i>
<i>Potentilla erecta</i>	<i>Buxbaumia aphylla</i> (a group of female plants on the side of a small hollow in the peat)
<i>Blechnum spicant</i>	<i>Campylopus flexuosus</i>
Occasional (not present in all plots; percentage absence from $\frac{1}{10}$ sq.m. samples greater than 95, but density not less than 10 plants per acre):	<i>Ceratodon purpureus</i>
<i>Trientalis europaea</i>	<i>Dicranum scoparium</i>
<i>Rumex acetosella</i>	<i>Hypnum cupressiforme</i>
<i>Festuca ovina</i>	<i>Leptodontium flexifolium</i>
<i>Agrostis tenuis</i>	<i>Leucobryum glaucum</i>
<i>Sieglingia (Triodia) decumbens</i>	<i>Mnium cuspidatum</i>
<i>Luzula pilosa</i>	<i>M. hornum</i>
<i>Carex binervis</i>	<i>Polytrichum juniperinum</i>
<i>C. flacca</i>	<i>P. piliferum</i>
	Hepaticae:
	<i>Calypogeia arguta</i>
	<i>Cephalozia bicuspidata</i>

(Percentage absence values were calculated from 240 samples of $\frac{1}{10}$ sq.m. in the area of 6 acres.)

Where the ground had been disturbed and the sandy subsoil exposed, as, for example, in front of old rabbit burrows, a rather different society was developed, including some of the above species together with others confined to this 'niche':

<i>Agrostis canina</i>	<i>Chamaenerion (Epilobium)</i>	<i>Galium verum</i>
<i>A. tenuis</i>	<i>angustifolium</i>	<i>Potentilla erecta</i>
<i>Aucumone nemorosa</i>	<i>Festuca ovina</i>	<i>Sagina procumbens</i>
<i>Anthoxanthum odoratum</i>	<i>Galium saxatile</i>	<i>Viola riviniana</i>

(c) *Design of experiment*

The whole hillside was burnt in March 1944, and again in the middle of April, in order to destroy as much as possible of the vegetation. Over the experimental area, excepting portions shaded in Fig. 1, this severe burning was sufficient to kill the great majority of rootstocks of *Calluna vulgaris* and *Erica cinerea*, and to destroy perennial plants (with the possible exception of some rhizomes of *Vaccinium* spp. and *Blechnum spicant*). Over the shaded regions, due to some heterogeneity in the previous treatment of the area, the vegetation was in a younger and fresher state just before burning, and consequently the fire was less effective. These areas were easily picked out from the rest, owing to the much greater cover of various species of grass and the obvious regeneration of *Calluna* and *Erica* from old rootstocks. They were neglected in the examination of the experiment, and,

although it is impossible to determine whether they affected grazing intensity on the rest of the plots in which they occurred, there was no evidence of this from observation of the sheep.

In July 1944, the experimental area was surrounded by a sheep fence, and the 6 acres thus enclosed were left ungrazed for a year. This fence was replaced in July 1945 by one proof also against rabbits, and the $\frac{1}{2}$ -acre plots laid out with sheep-fencing as shown in the plan (Fig. 1). Rabbits are from time to time found in the enclosure, but are removed whenever detected.

The treatments were duplicated, and the plots in each replicate arranged at random (with the exception that plots grazed only in daytime were of necessity sited next to those grazed only at night to allow convenient transfer of the sheep from one to the other).

The following treatments were adopted:

- | | |
|---------------------------------------|--|
| (1) Control, ungrazed | |
| (2) Grazing by day | } The yearly average for these plots amounted to a fairly mild grazing intensity |
| (3) Grazing by night | |
| (4) Heavy winter grazing | |
| (5) Heavy summer grazing | } These plots were severely overgrazed |
| (6) Heavy grazing throughout the year | |

The 'winter' grazing period lasted from 20 October to 15 April; and the 'summer' period from 15 May to 20 October. All plots were rested during the months of February and March, and in 1947, owing to the unusually hard weather, there was also no grazing in April and May.

Grazing commenced in September 1945, and the intensities are recorded in Table 2 in 'sheep-days'. Grazing was not continuous, and the number of sheep introduced varied between eight and ten to a plot, but if, for example, nine sheep were grazed on one plot for 4 days (i.e. four periods of 24 hr.), this was recorded as 36 sheep-days. It was not found possible to maintain the grazing intensity of each treatment at an exactly constant level throughout the 2 years' duration of the experiment. Consequently, for each set of observations the grazing intensity is shown as the average number of sheep-days per plot per year, calculated for the period from the start of the experiment to the date of the particular observation.

Table 2. *Grazing treatment in 'sheep-days'*

		Non-effective months have been omitted.															
		1945		1946								1947					
		S.	O.	Ja.	Ap.	Ju.	Jul.	Au.	S.	O.	N.	D.	Ja.	Ju.	Jul.	Au.	Total
1. Control, ungrazed	A	0
	B	0
2. Grazing by day	A	41	.	27½	10	15	20	20	20	20	15	10	5	10½	7	20	241
	B	45	.	27½	13½	15	20	20	20	20	15	10	5	9	6	22½	248½
3. Grazing by night	A	43	.	27½	10	15	20	20	20	20	15	10	5	10½	7	20	243
	B	45	.	27½	13½	15	20	20	20	20	15	10	5	9	6	22½	248½
4. Heavy winter grazing	A	.	.	65	36	60	60	50	.	.	.	271
	B	.	.	65	40	60	60	50	.	.	.	275
5. Heavy summer grazing	A	60	.	.	.	40	40	50	30	42	.	.	.	38½	35	36	371½
	B	60	.	.	.	40	40	50	30	44	.	.	.	33	50	36	383
6. Heavy grazing throughout the year	A	54	24	60	27	20	40	30	30	18	30	10	10	15	18	18	404
	B	48	24	40	20	20	40	30	30	16	30	10	10	17½	16	18	369½

(Plots belonging to the upper replicate are labelled A; those to the lower, B.)

(d) Results

Examination of the control plots showed that during the period of the experiment a stage of recolonization in which *Erica cinerea* and *Calluna vulgaris* formed an almost closed community had been reached. *Carex pilulifera* was scattered abundantly throughout, and to a lesser degree *Deschampsia flexuosa* and *Luzula multiflora*. All other species played only a subordinate role.

The effects of grazing upon the structure of this type of community do not lie in any significant change in the specific composition, but rather in changes in the proportions of the constituent species and in particular in the balance between the two dominants.

Over the greater part of the experimental area re-establishment of *Erica* and *Calluna* was entirely from seed. The young plants of both species were freely grazed and there was no evidence that sheep discriminated between the two at this early stage. No particular effect due to the season at which the plots were grazed could be detected in the reactions of the two species. There was, however, a direct response to grazing intensity, both in height and general appearance, the data for which are presented in Table 3. Two further comparisons of performance in the various plots demonstrate the nature of the effects of grazing on the vegetation.* These were made as follows:

(i) By weighing the total (air-dried) *Erica* and *Calluna* gathered from random sample areas† on three occasions (12 October 1946; 26 May and 4 October 1947) and plotting the weight per $\frac{1}{10}$ sq.m. against the grazing intensity. The results (Fig. 2) show an inverse relationship between the previous grazing treatment and the weight per unit area.

Table 3. *Measurements and field notes: Glensauagh, 13 July 1946 and 4 October 1947†*

		Average height of stand of <i>Erica cinerea</i> and <i>Calluna vulgaris</i> (in.)	Field notes	Average no. of sheep-days per plot per year (period Sept. 1945 to Sept. 1947)§
1. Control, un-grazed	A	3-6}	Strong even stand giving a good and fairly uniform cover. Bright green appearance from distance	0
	B	3-8}		0
2. Grazing by day	A	$\frac{1}{2}$ -1}	Bare ground evident, especially on steep parts. Greenish appearance	115.7
	B	$\frac{1}{2}$ -2}		119.3
3. Grazing by night	A	$\frac{1}{2}$ -1}	Much bare ground, but greenish from distance	116.6
	B	1-2}		119.3
4. Heavy winter grazing	A	2-5}	Good green cover grown up during summer when un-grazed. Bare ground only on steepest parts	130.1
	B	1-3}		132.0
5. Heavy summer grazing	A	$\frac{1}{2}$ -1}	Considerable amount of bare ground. Greenish brown appearance	178.3
	B	$\frac{1}{2}$ -1}		183.8
6. Heavy grazing throughout the year	A	$\frac{1}{2}$	Much bare ground. Plots appear brown from distance	193.9
	B	$<\frac{1}{2}$		177.4

‡ Almost identical records were obtained in the two successive years.

§ See p. 104.

(ii) By counting the total number of flowering racemes of *Erica* and *Calluna* in twenty $\frac{1}{10}$ sq.m. random samples per plot in October 1946 and 1947. The results (Fig. 3) show

* Such direct comparisons involve the assumption that all plots were initially identical. With the exceptions already discussed the whole area had been subjected to severe burning, and at the start of the experiment all plots were therefore alike in being largely bare of all vegetation.

† See p. 107 for sampling methods.

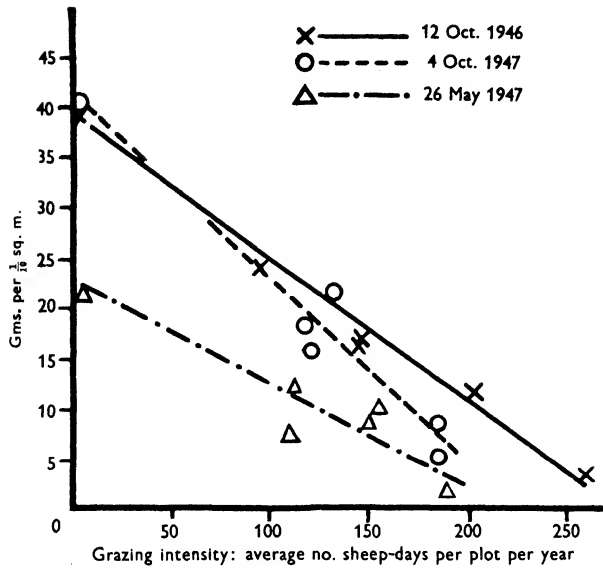


Fig. 2. Relationship between grazing intensity and total weight of vegetation per unit area: Glensaugh. (The line representing May falls lower than those representing October owing to the shorter period of growth prior to sampling.)

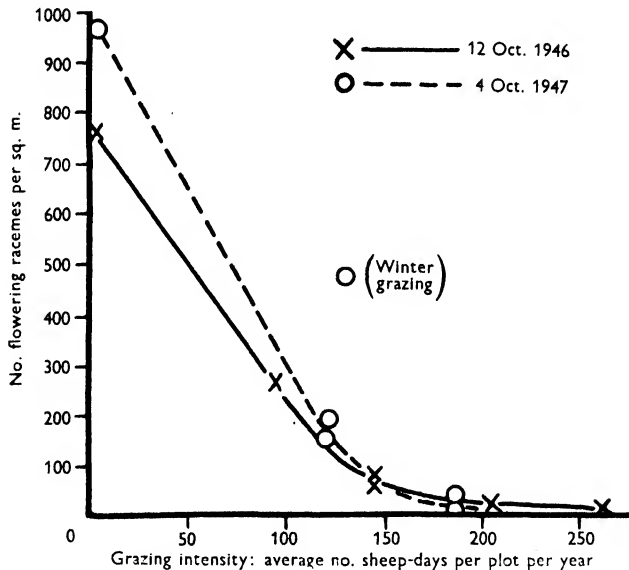


Fig. 3. Relationship between grazing intensity and number of flowering racemes of *Erica cinerea* and *Calluna vulgaris*: Glensaugh. (The abnormally high figure from the winter grazing plots in 1947 probably results from the absence of April grazing owing to snow.)

a close inverse relationship between grazing intensity and flowering, on which the adverse effect of grazing is relatively severe.

The foregoing observations illustrate the general response of the two codominants to the

biotic factor. It was, however, early apparent that the balance between them was directly affected by the intensity of grazing. This relationship was investigated in two ways:

(i) The proportion in which the two species became established as seedlings was first determined. Small areas were located in each plot containing young seedlings only. The number of seedlings of each species occurring in two samples ($\frac{1}{100}$ sq.m. each) of such areas in each plot was counted. Table 4 shows that seedling establishment of *Erica* was consistently higher than that of *Calluna*, the figures varying between approximately two and five times greater. The totals do not vary significantly according to treatment and show an average total seedling density of about 13,600 individuals of both species per square metre.*

Table 4. *Number of seedlings in two samples of $\frac{1}{100}$ sq.m., 20 September 1946*

	A replicate	B replicate	Total (in 4 samples)	Average no. of sheep-days per plot per year (period Sept. 1945 to Sept. 1946)†
1. Control, ungrazed:				
<i>Erica</i>	246	124	370	0
<i>Calluna</i>	121	78	199	
2. Grazing by day:				
<i>Erica</i>	127	219	346	145.2
<i>Calluna</i>	71	20	91	
3. Grazing by night:				
<i>Erica</i>	78	270	348	146.1
<i>Calluna</i>	77	26	103	
4. Heavy winter grazing:				
<i>Erica</i>	320	308	628	95.1
<i>Calluna</i>	74	53	127	
5. Heavy summer grazing:				
<i>Erica</i>	86	239	325	203.1
<i>Calluna</i>	54	25	79	
6. Heavy grazing throughout the year:				
<i>Erica</i>	225	237	462	247.8
<i>Calluna</i>	136	49	185	

† See p. 104.

(ii) The balance between the two species in the fully developed vegetation of each plot was next determined by comparing their weights in material gathered from random sample areas. (This method proves particularly suitable when comparing the performance of two species of closely similar life-form under varying treatments.) The preliminary samples were taken on 12 October 1946, from two quadrats of $\frac{1}{10}$ sq.m. in each plot. The operation was repeated on two later occasions (26 May 1947, and 4 October 1947) when the sampling method was changed to ten rectangular (see Clapham, 1932) quadrats of $\frac{1}{100}$ sq.m. in each plot in order to cover the area more adequately. Consistent results were obtained, however, on all three occasions. The samples were allowed to dry for at least 4 weeks in a warm laboratory before weighing. The results appear in Table 5 and Fig. 4.

The figures and curves demonstrate that, whereas in the ungrazed plots *Erica* shows a considerably greater weight per unit area than *Calluna*, the reverse is true for the great majority of grazed plots; and in the few cases in which *Erica* retains the higher weight in a grazed plot the difference is much reduced. The effect of grazing is, therefore, to reverse the dominance of *Erica* over *Calluna*, and this reversal takes place (as shown by the upper points of intersection of the curves) with a minimum treatment of between 50 and 100

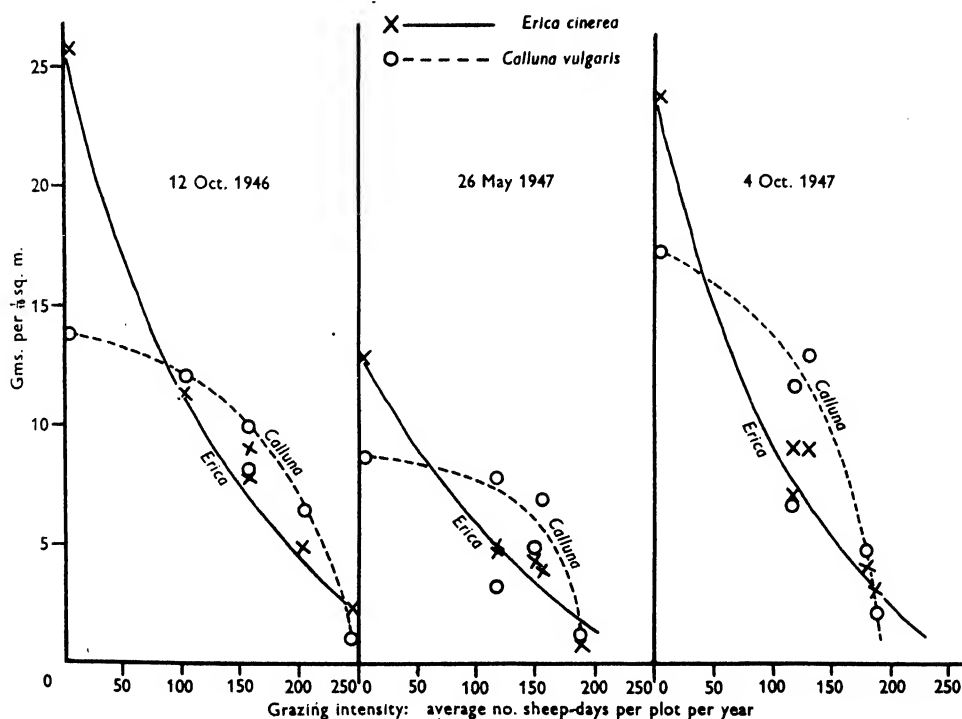
* In a neighbouring 8-year-old stand density was approximately 20 plants per square metre.

Effects of sheep-grazing on vegetation

Table 5. Effect of grazing intensity on the balance between *Erica cinerea* and *Calluna vulgaris*

Weight of air-dried samples expressed in grams per $\frac{1}{16}$ sq.m.						
12 Oct. 1946			26 May 1947		4 Oct. 1947	
Weight	Average no. of sheep-days per plot per year (period Sept. 1945 to Sept. 1946)*		Weight	Average no. of sheep-days per plot per year (period Sept. 1945 to May 1947)*	Weight	Average no. of sheep-days per plot per year (period Sept. 1945 to Sept. 1947)*
1. Control, ungrazed:						
<i>Erica</i>	25.84	0	12.81	0	23.77	0
<i>Calluna</i>	13.91		8.63		17.21	
2. Grazing by day:						
<i>Erica</i>	9.13	145.2	4.71	118.4	7.18	117.5
<i>Calluna</i>	7.81		3.12		11.62	
3. Grazing by night:						
<i>Erica</i>	7.73	146.1	4.92	119.0	9.13	118.0
<i>Calluna</i>	9.89		7.71		6.74	
4. Heavy winter grazing:						
<i>Erica</i>	11.28	95.1	3.91	156.0	9.13	131.0
<i>Calluna</i>	12.19		6.77		12.92	
5. Heavy summer grazing:						
<i>Erica</i>	4.97	203.1	4.39	150.3	4.03	181.1
<i>Calluna</i>	6.64		4.79		4.67	
6. Heavy grazing throughout the year:						
<i>Erica</i>	2.40	247.8	0.92	191.7	3.15	185.6
<i>Calluna</i>	1.07		1.09		2.18	

* Average number of sheep-days per plot per year calculated separately for the period prior to each date of sampling (see p. 104).

Fig. 4. Effect of grazing intensity on the balance between *Erica cinerea* and *Calluna vulgaris*: Glensnaugh.

sheep-days per plot per year. Under conditions of previous treatment of 100 sheep-days per plot per year and over, *Calluna* shows the greater weight per unit area, until the severity of grazing becomes so great that the curves converge and only relatively small quantities of either species survive. The curves, however, cross a second time at a grazing intensity of between 190 and 240 sheep-days per plot per year, indicating that above this intensity *Erica* may once more become slightly more vigorous than *Calluna*.

(e) *Discussion*

It has been shown that on the experimental area *Erica* became established as seedlings in greater density than *Calluna*, and that in the ungrazed plots *Erica* maintained a greater weight per unit area throughout the period of the experiment. Both with regard to the effect upon community structure and to the practical application of the findings, the most important result of introducing grazing of varying intensity was to alter this balance between the two codominants. Grazing at an intensity between the limits of 50 and 200 sheep-days per plot per year (approximately equivalent to limits of not less than one sheep to 4 acres and not more than one sheep to 1 acre throughout a year) shifted the balance in favour of *Calluna*. This suggests the optimum level of grazing intensity for maintaining upland heath of this kind in the most valuable condition (i.e. with *Calluna* dominant) after burning. At still higher grazing intensities in the overgrazed plots it would appear, however, that *Calluna* drops out rather more quickly than *Erica*.

A community dominated by *E. cinerea* is generally regarded as a normal seral stage in the recolonization subseries on dry upland heath, giving place in time to Callunetum (Elgee, 1914; Tansley, 1939). The effect of sheep-grazing (excluding severe overgrazing) under the conditions described is to accelerate the assumption of dominance by *Calluna*, to the exclusion of the *Erica*-dominated seral stage.

An outstanding problem arises as to the reasons for this differential response to grazing in *Erica cinerea* and *Calluna vulgaris*. The experiments to be described in §III were designed to test an indication derived from field observations that this response may be determined by different reactions of growth morphology to grazing.

III. LABORATORY EXPERIMENTS

A series of observations and experiments was carried out to compare the growth-form of the two species under identical conditions and under experimental imitation of grazing, with a view to the possible interpretation of the field results on this basis.

Owing to its taxonomic interest as a monotypic genus, much work has been devoted to *Calluna* from all aspects. Nordhagen (1937–8) has considered its taxonomic and geographical relationships and the morphology and biology of its reproduction, while Beijerinck (1940) has devoted a monograph to its morphology, life history, ecology and geography. In these works (especially the second) there are full descriptions of the general morphology of *Calluna*, its types of branching, the relationships between the long shoots and short shoots and their duration, and the general life history from the seedling stage to the assumption either of a hemispherical dwarf-shrub habit or of a 'dwarf-tree' form according to environmental conditions. There are, however, only passing references to details of the early stages of growth (i.e. during the first two years), and the effects of the

destruction of the apex of the main axis are mentioned only in general terms. In the case of *Erica* no complete description of growth morphology is available.

For these reasons the following investigations form a detailed study of the main features of growth morphology during the early stages of development in the two species. The bulk of the data refers to the first year of growth, since the majority of plants in the field experiment were grazed at a very early stage, and field conditions were imitated as far as possible in order to reach a valid interpretation of field results.

(a) *Method*

Seeds of the two species were picked out from floral debris, surface sterilized with calcium hypochlorite, and germinated on pads of glass-wool standing in Petri dishes containing distilled water.* The germinated seeds were then transferred to pads of glass-wool standing in Pfeffer's solution, on which they were grown until they had produced about two pairs of leaves (approximately 6 weeks) and were large enough to plant out. At this stage the main root was unbranched or had only one or two simple branches, and the seedlings could easily be lifted from the glass-wool and planted in pots or boxes. The soil used was the surface soil taken from the experimental area. The plants were grown in an unheated greenhouse, and during the first month after planting a moist atmosphere was maintained by covering with small bell-jars or sheets of glass. These were removed when the seedlings were well established, and throughout the period of observation the plants remained perfectly healthy and none of the untreated seedlings died. Experimental imitation of grazing was carried out by cutting and removing all parts of the seedling above the stated level with a pair of scissors.

(b) *Comparison of early stages of growth in Erica cinerea and Calluna vulgaris*

Table 6 shows that there is very little difference in behaviour between the two species during the earliest weeks of growth. Under the cultural conditions the cotyledons of *Erica* become expanded slightly more rapidly than those of *Calluna*, but in both the first pair of leaves appears approximately 20 days later and the second after a somewhat shorter interval. Subsequent pairs follow more rapidly, especially in *Calluna*, in which intervals of 4-6 days were noted between the full expansion of successive pairs, as compared with the usual 7 in *Erica*. In the latter the slower rate may be correlated with the larger size of leaf and greater elongation of internode.

Until about 6 weeks after planting (or 12 weeks after germination) seedlings of both species grow vertically upwards from the single active apex. The rates of growth are approximately equal, although *Erica* increases in height slightly more rapidly than *Calluna* (Pl. 2, phot. 1). At this stage, however, when the *Calluna* seedlings are about 10 mm. high, they begin to form lateral branches from axillary buds, while *Erica* continues upward growth. The first laterals most frequently appear from the axils of one of the sixth to tenth pairs of leaves, not from the lowest pair. This fact has considerable significance later in development. After the first lateral (or pair of laterals) has appeared, others develop at short intervals up the stem in a more or less regularly decussate fashion, producing the typical 'spruce-like' form of the young *Calluna* plant (Pl. 2, phot. 2). From then onwards, as the

* Seeds of *Calluna* germinated freely in the dark. This is not in agreement with a statement by Beijerinck (1940, p. 60). *Erica cinerea*, however, required light for germination.

main apex continues to grow and produce successive leaf-pairs, at more or less regular intervals a pair of axillary buds commences growth, maintaining the regular sequence of laterals which grow obliquely upwards at an angle of 20–30° to the horizontal.

Table 6. *Comparative chronology of early stages of untreated Erica cinerea and Calluna vulgaris*

Under each species the left-hand column indicates the age at which the largest number of individuals reached the stage shown, while the right-hand column gives the range of times taken to proceed from one stage to the next.

	<i>Erica cinerea</i>		<i>Calluna vulgaris</i>	
	Days from germination	Days from preceding stage	Days from germination	Days from preceding stage
Cotyledons fully expanded	7 (first, 3 days; last, 14 days)		14 (first, 7 days; last, 17 days)	
Leaves fully expanded: 1st pair	30	20–24	35	20–22
2nd pair	45	14–16	46	10–12
3rd pair	52	7	50	4–5
4th pair	59	7	55	4–6
5th pair	67	7–10	60	4–6
6th pair	75	7–10	66	5–7
	Weeks from germination		Weeks from germination	
Beginning of 1st lateral	16 (first, 12 weeks; last, 20 weeks)		12 (first, 10 weeks; last, 16 weeks)	
Height of plant when 1st lateral produced (mm.)	35 (shortest, 28; tallest, 42)		10–12 (shortest, 8; tallest, 16)	

In *Erica*, however, branching does not commence until about 15–16 weeks after germination, when the seedlings are approximately 35 mm. high (Pl. 2, phot. 2). The position of the first branch appears to vary considerably, but as in *Calluna* it is generally above the first-formed leaves. Although a general sequence of development with the oldest and longest branches at the base follows, the more or less regular decussate arrangement of *Calluna* is lacking, and the branches are fewer and more widely spaced, and normally grow obliquely only for a very short distance and then turn more or less vertically upwards. The difference in the habit of young plants of the two species at an age of about 18 weeks can be seen in Pl. 2, phot. 3.

At about 21 weeks from germination an additional development appears in *Calluna*. The buds in the axils of the few pairs of leaves at the very base below the oldest branches now become active, giving rise to a dense tuft of young branches below the rest of the branch system. The regular 'spruce-like' form is further modified by the fact that the oldest branches near the base of the young plant grow rather more rapidly than the rest, often more or less horizontally, spreading over the ground. Both tendencies are clearly shown in Pl. 2, phot. 4 which illustrates the stage reached by the end of the first growing season.

At a similar stage *Erica* exhibits a much less regular growth-form with fewer, longer branches at irregular intervals up the stem, adopting a more or less vertical direction of growth. A few younger branches have appeared from close to the base, growing more or less vertically upwards, but no dense tuft is formed as in *Calluna* (Pl. 2, phot. 5).

The result at the end of one season's growth in both species is a young plant still showing a leading shoot. In *Erica*, however, an irregular, narrowly ascending growth-form develops, while *Calluna* is characterized by a regular pyramidal and spreading form, with a

considerable potentiality for growth from the base. The percentage cover given by the young plant is considerably greater in *Calluna*.

(c) *Response to cutting*

Experiment 1. Single cut at 1 cm. above soil surface, 10–16 weeks from germination.

It was estimated that in a compact, close-cropped community, such as was produced on any of the grazed plots in the field experiment, a sheep would sever plants at approximately 1 cm. from the soil surface. The position of the experimental cut was chosen accordingly, and as young plants 10–16 weeks old were not, or only slightly, higher than 1 cm., this frequently involved the removal of a very small portion of the apex only.

The response of the two species to this treatment differed strikingly.

Erica. Of twenty-nine seedlings, all except two (to which apparently negligible damage was done since growth was unaffected) produced generally two secondary growing apices from just below the cut, 3 weeks later. These grew at approximately equal rates and remained equivalent at least during the rest of the growing season, at first assuming a divergent direction of growth and later becoming erect (Pl. 3, phot. 6). About 7 weeks after cutting, one to three buds normally appeared in the axils of the lowermost leaves on the original stem below the cut (also shown in Pl. 3, phot. 6). These assumed a vertical direction of growth, and by the end of the season one or more were sometimes approaching the height of the two original branches, which were beginning to produce laterals as in untreated plants.

Calluna. All treated plants showed an acceleration in the production of laterals as compared with the controls. With regard to growth-form, however, two distinct types of response were obtained, both different from that in *Erica*.

(i) 'Spreading' response. Of thirty-nine treated plants, twenty-five developed from one to three buds which, during the following months, assumed a horizontal plagiotropic form of growth, producing a series of plants of a prostrate, creeping habit (Pl. 3, phot. 7). The striking difference between this response and that in *Erica* can be seen in Pl. 3, phot. 8, in which treated specimens of the two species growing side by side may be compared. Laterals were produced from these creeping shoots in the normal manner, and frequently grew more or less vertically upwards. In addition, about 7 or 8 weeks after cutting, a tuft of branches from the base of the original stem below the cut became evident, and grew obliquely upwards in the same way as the secondary set of branches from the axils of the lowest leaves in untreated plants. The result at the end of the growing season was a plant with one to three extensive plagiotropic axes themselves freely producing laterals, radiating from a dense tuft of young upgrowing branches developed on the original stem base (Pl. 3, phot. 9). Such a plant gives very considerable cover in proportion to its bulk.

(ii) 'Bushy' response. The remaining fourteen plants, however, produced no plagiotropic axes, but showed either a small number of erect or oblique branches with numerous laterals, or a tuft of five to eighteen upgrowing branches. The result at the end of the season in either case was a small, densely tufted and richly branched form (Pl. 4, phot. 10).

Experiment 2. Single cut at 1 cm. above soil surface, 20–22 weeks from germination.

Here the seedlings used were appreciably older than in Exp. 1.

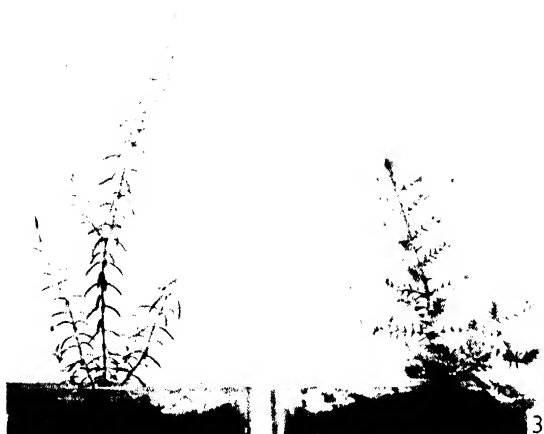
Of fourteen plants of *Erica* treated in this way no difference in response from that described in the case of Exp. 1 was observed.



Phot. 1. Seedlings aged approx. 12 weeks.
Left, *Calluna*; right, *Erica*. ($\times 1$.)



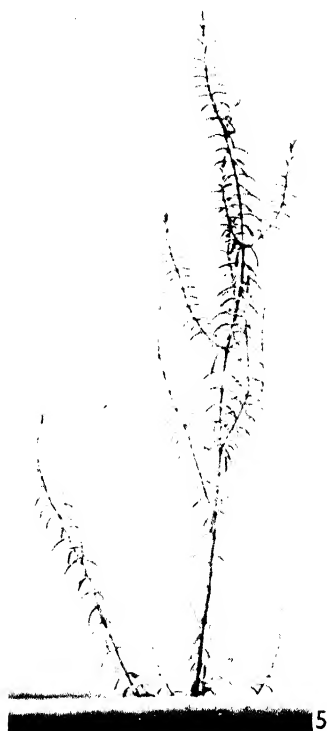
Phot. 2. Plants aged approx. 15 weeks.
Left, *Erica*; right, *Calluna*. ($\times 1$.)



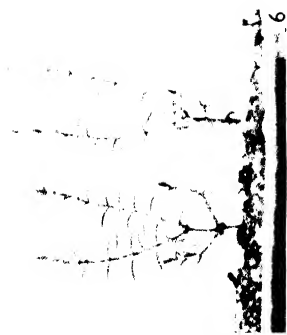
Phot. 3. Plants aged approx. 18 weeks.
Left, *Erica*; right, *Calluna*. ($\times 1$.)



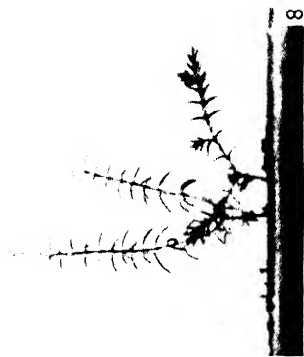
Phot. 4. *Calluna* aged approx. 30 weeks. ($\times 1$.)



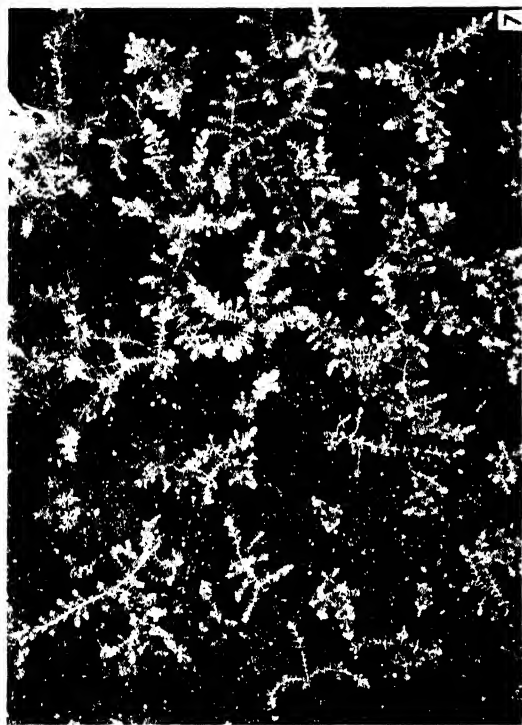
Phot. 5. *Erica* aged approx. 30 weeks. ($\times 1$.)



Phot. 6. *Erica* cut to 1 cm. at approx. 10 weeks, photographed 16 weeks later. ($\times 1$.)



Phot. 8. Seedlings cut to 1 cm. at approx. 10 weeks, photographed 16 weeks later. Left, *Erica*; right, *Calluna*. ($\times 1$.)



Phot. 7. *Calluna*: cutting to 1 cm. performed at various times between the ages of 13 and 16 weeks. Viewed from above, 16 weeks after earliest cutting. ($\times \frac{1}{3}$.)



Phot. 9. 'Spreading' response in *Calluna*; seedling cut to 1 cm. at approx. 13 weeks, photographed 24 weeks later. ($\times 1$.)



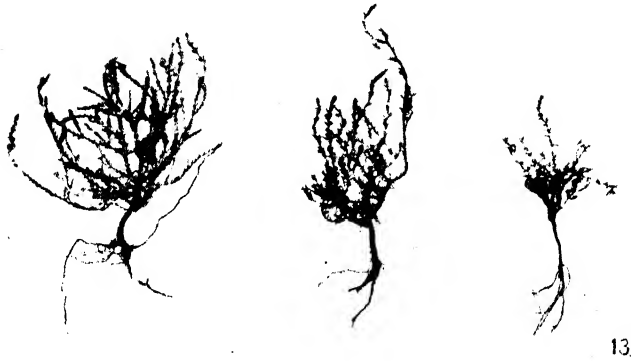
Phot. 10. 'Bushy' response in *Calluna*; seedling cut to 1 cm. at approx. 20 weeks, photographed 20 weeks later. (Slightly enlarged.)



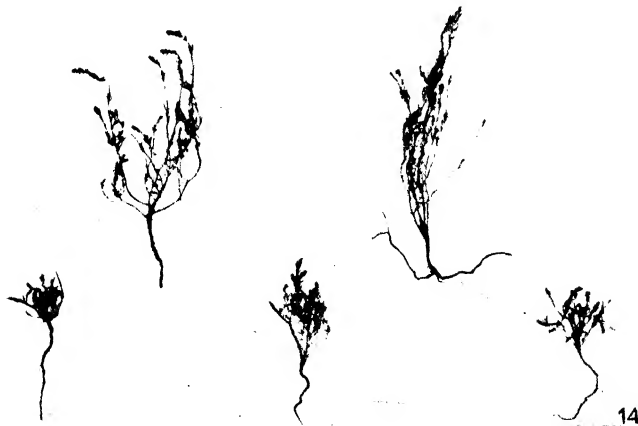
Phot. 11. *Erica* from field experiment; forms with few upgrowing branches as found abundantly on mildly grazed plots (cf. Phot. 6). ($\times \frac{1}{2}$.)



Phot. 12. *Calluna* from field experiment; spreading form as found abundantly on all grazed plots (cf. Phot. 9). ($\times \frac{1}{2}$.)



Phot. 13. *Calluna* from field experiment; bushy form as found on all grazed plots (cf. Phot. 10). ($\times \frac{1}{2}$.)



Phot. 14. *Erica* from field experiment; bushy form as developed chiefly under severe grazing. ($\times \frac{1}{2}$.)

In *Calluna* the nine treated plants all showed the 'bushy' type of response, and in no case was the 'spreading' type observed.

Consideration of Exps. 1 and 2.

It would appear that the response to an imitation of grazing in the form of a single cut at 1 cm. above soil surface can be interpreted on the basis of the normal behaviour of laterals in untreated plants. The laterals of *Erica* in untreated plants grow obliquely for a very short distance only and then turn vertically upwards. The effect of destruction of the main apex appears to be the stimulation of the development of the buds in the axils of a pair of leaves below the cut. The resulting pair of axes behave in the way typical of lateral branches in *Erica*. Later the buds in the axils of a few of the lower leaves on the original stem may become active as in the normal plant.

In a normal *Calluna* seedling it was observed that the oldest branches usually grow rather more rapidly than the rest and become plagiotropic. In plants showing the 'spreading' response it is possible that the first branches to develop after cutting appear from the position on the stem from which these first laterals would have arisen if the leader had not been destroyed. Removal of the main apex here merely accelerates the development of these branches. The tuft of young branches developing later from the base of the original stem appears in all respects similar to that produced on normal plants.

An explanation of the 'bushy' response in the 10-16-week-old seedlings can be based on the slight variation in age and rate of growth of the individuals, involving the possibility that the young plants showing this response were cut across *below* the nodes from which the plagiotropic branches proceed. This would leave only the nodes normally producing a tuft of branches at a slightly later stage. The results of Exp. 2, in which all the 20-22-week-old seedlings showed the 'bushy' response, are in accord with this explanation, since it is likely that during the early growth of the young plant there is a slight elongation throughout, as well as just behind the meristem. At the older stage, therefore, there would be a greater chance of a cut at 1 cm. removing the nodes from which plagiotropic branches are derived, and eliciting the 'bushy' response.

The results of further experiments bear on this interpretation:

Experiment 3. Second cutting at 1 cm. above soil level.

The treatment as given in the previous experiments was repeated: on some plants at 20 days after the first cutting, on others 52 days later.

Records from only four plants of *Erica* are available. In two cases (one recut after 20 days, the other after 52) growth-form was unaltered. The others, both recut after 52 days, later showed four and five upgrowing branches.

Fifteen plants of *Calluna* were treated in this way, and two of those recut 20 days after the first treatment were subjected to a third cut 52 days later. In none of these plants was there any alteration in the form of the original response.

Experiment 4. Single cuts at various levels.

In *Erica* the response of the majority of treated plants was little affected by the level of cutting. One plant cut to within 4 mm. of the soil surface produced five erect branches and appeared similar to some examples of the effect of repeated cutting in Exp. 3.

In *Calluna*, however, the form of the response was directly related to the level of the cut.

Previous experiments showed that at an age of more than 20 weeks, plants cut to any level up to just over 1 cm. would show the 'bushy' response. However, when plants of this age were cut at 1.5 cm., two out of three plants gave the 'spreading' response. At higher levels than this only the 'spreading' response occurred. On the other hand, some specimens severely cut to within 4 mm. of the soil surface failed to produce the full 'bushy' response and gave rise to two upgrowing branches only.

(d) *Discussion*

The results of Exps. 3 and 4 confirm and extend the conclusions reached on the basis of Exps. 1 and 2. The typical response of a young *Erica* plant to the imitation of grazing is the development of a small number of branches which rapidly assume an upward direction of growth. After several weeks buds from the lower nodes may become active (as in untreated plants), and by the end of the growing season (e.g. after 7 months) these lower branches may approach the height of the original ones. The resulting plant gives the appearance of a rather loose bushy form composed of relatively few erect axes. Plants which have been severely cut back or which have been cut more than once appear sometimes to adopt a rather denser bushy form, showing four or five active apices. It is probable that in these cases the node normally producing the first rapidly growing branches has been removed, leaving only those which normally develop later. Growth from these was evidently initiated immediately in the absence of any active apices at a higher level.

The fact that 20-week-old *Calluna* plants produced the 'spreading' response if the cutting level was raised to 1.5 cm. supports the conclusion that this response develops when the nodes immediately below the cut are those which would produce the lower plagiotropic branches in a normal plant. If, however, these nodes are removed, activity of the lower buds is initiated, these being ones which normally produce a tuft of upgrowing branches at the base. In this way the 'bushy' response develops. (When the cutting level is such that only the cotyledons and one higher node remain, a response rather similar to that of *Erica* results, since it appears that only two buds capable of growth are left.)

The fact that the type of response is unaltered by further cutting at the same level is in accordance with this explanation, since after the first cut which determines the initial type of response there is little increase in length in the remainder of the original stem, growth taking place in the branches. Further treatment will merely cut back these branches, while the nodes on the original stem remain unaffected. Since it is the behaviour of branches from these nodes which determines the form of response, the only effect of further cutting is to intensify the expression of the response already elicited.

IV. INTERPRETATION OF FIELD RESULTS

Use of the foregoing experimental results in the interpretation of the field data is permissible only if growth-forms similar to those produced artificially are evident in the field. Pls. 4 & 5, phot. 11-14, illustrating samples taken from grazed plots in the field experiment, show growth-forms closely similar to the main types produced under cultural conditions. All plants in samples from the field experiment can be recognized either as ungrazed, or as belonging to one or other of these types.

(a) *Interpretation of field data on the basis of morphological response to grazing*

It was shown that, after burning, *Erica* becomes established from seed on the hillside in greater numbers than *Calluna*, and that on the control plots this dominance is maintained for at least 3 years. Under conditions of medium grazing this dominance is reversed.

Under medium cutting in culture *Erica* produces a few erect branches, later supplemented by a small number of additional ones from lower nodes, resulting in a loose bushy form with relatively few growing axes. Such a form gives only a slightly greater percentage cover than that of an undamaged plant, while it is susceptible to considerable damage from further grazing. It is reasonable to assume, however, that the predominant response of *Calluna* under mild grazing will be the 'spreading' one, since where the forage is relatively abundant the herbage is less closely grazed by sheep. This growth-form not only gives considerably greater percentage cover than a grazed *Erica* of the same age, but, in addition, the main growing apices, being plagiotropic, are less likely to be damaged by further grazing. In this manner *Calluna* may gradually obtain a competitive advantage over *Erica*.

Even under conditions of rather severer grazing, when the main form of response in *Calluna* would be the 'bushy' one, the tuft formed is denser than that of *Erica* and is composed of a larger number of branches. A competitive advantage may be maintained even by this form, with regard both to percentage cover and to susceptibility to further grazing.

If, however, *Erica* is very closely or repeatedly grazed, as would be the case in the severely overgrazed plots, the experimental evidence suggests that a more densely bushy form may result, of a type somewhat similar to that occurring in *Calluna*. Such a form occurs on the experimental plots and is shown in Pl. 5, Phot. 14. This reaction may account for the greater representation of *Erica* under the heaviest grazing intensities.

(b) *Verification of interpretation*

In verification of this interpretation, the relative proportions of the different growth-forms under the various intensities of grazing were estimated. Samples of plants were pulled from randomly selected sites in each plot. The two species were separated and the individuals classified into three groups: erect, spreading and bushy.

The erect group contained plants showing a small number of erect axes (normally between one and six), including in both species the undamaged plants, and in the case of *Erica* the lightly grazed plants also, which showed two or three upgrowing branches or had produced the loose bushy form. The size of this group shows the proportion of plants which give little cover and are susceptible to considerable damage by further grazing. The spreading form was readily recognized, and the bushy class was limited to the dense tuft of erect or oblique branches. The relative proportions of the three groups under the various grazing intensities appear in Table 7.

In the ungrazed plots the erect class contains between 80 and 90% of individuals in both species, the small proportions in the spreading and bushy groups presumably being due to accidental damage to the main apex. As would be expected from the experimental results, the proportion of erect plants in *Erica* is always higher than in *Calluna*, whatever the treatment. The spreading response is practically absent in *Erica* and, although a few plants from most samples showed a form which was classified as spreading, it contributed

an unimportant proportion and was in no way a distinct reaction as in *Calluna*. The bushy response, however, forms an appreciable proportion in all samples of *Erica* from grazed plots, and reaches a significantly higher proportion in the plots which were overgrazed throughout the year.

Table 7. *Proportions of growth-form types in relation to grazing treatment: Glensaugh 25 June 1947*

		Average no. sheep-days per plot per year (period Sept. 1945 to June 1947)*	Erica				Calluna			
			Total no. of plants	% of total			Total no. of plants	% of total		
				Erect	Spread- ing	Bushy		Erect	Spread- ing	Bushy
1. Control, ungrazed	A	0	66	81.8	0	18.2	34	88.2	8.8	2.9
	B	0	70	78.6	1.4	20.0	30	86.6	6.7	6.7
	Mean	0		80.2	0.7	19.1		87.4	7.7	4.8
2. Grazing by day	A	116.7	59	69.5	1.7	28.8	54	16.7	48.1	35.2
	B	120.0	74	73.0	5.4	21.6	35	31.4	54.4	14.3
	Mean	118.4		71.2	3.5	25.2		24.0	51.2	24.7
3. Grazing by night	A	117.8	18	33.3	5.5	61.1	49	24.5	28.6	46.9
	B	120.0	151	90.0	2.7	7.3	15	46.7	33.3	20.0
	Mean	118.9		61.6	4.1	34.2		35.6	30.9	33.4
4. Heavy winter grazing	A	147.8	84	73.8	0	26.2	40	50.0	32.5	17.5
	B	150.0	75	66.7	5.3	28.0	77	45.4	35.1	19.5
	Mean	148.9		70.2	2.6	27.1		47.7	33.8	18.5
5. Heavy summer grazing	A	163.9	59	57.5	3.4	39.0	28	28.6	53.6	17.8
	B	162.0	87	80.5	3.4	16.1	17	17.6	47.1	35.3
	Mean	163.0		69.0	3.4	27.5		23.1	50.3	26.5
6. Heavy grazing throughout the year	A	200.7	42	45.2	11.9	42.9	18	5.5	66.7	27.8
	B	183.0	55	41.8	1.8	56.4	15	13.3	53.3	33.3
	Mean	191.9		43.5	6.8	49.6		9.4	60.0	30.5

Figures from A and B replicates show no significant differences and have therefore been combined for the purpose of analysis (with the exception of those for *Erica* in treatments 3 and 5 which show an unexplained difference). All the differences commented on in the text have been shown to be significant.

* See p. 104.

In *Calluna* the proportion of erect plants in all grazed plots is significantly lower than in the controls, and when overgrazed throughout the year, averages less than 10%. The spreading and bushy responses, however, both show significantly higher proportions under grazing than in the controls, particularly at the higher intensities.

Analysis of the relative proportions of the various growth-form types produced under field conditions therefore provides satisfactory verification of the suggested explanation of the changing balance between the two species.

(c) *Later stages of development*

Little information about the subsequent behaviour of the two species under continued grazing is yet available. Both Nordhagen and Beijerinck, however, refer to the fact that in time, even in undamaged *Calluna* plants, the original main apex ceases to grow and the organization becomes sympodial, with the production at an age of 5 or 6 years of a hemispherical or 'shrubby' type of plant. Older individuals of *Erica* also show no leading shoot, but owing to the more open type of branching the resulting shrub is much less dense. It is therefore possible that, even in the absence of grazing, *Calluna* would eventually gain

a competitive advantage over *Erica* and reverse the dominance. This may relate to the recorded fact that in certain areas a community dominated by *Erica* is a seral stage in the establishment of *Callunetum*. If this applies to the locality in which the experiment described here is situated, then the effects of grazing may be regarded as an acceleration of the seral changes.

Some evidence of such a change in growth-form is found on the ungrazed plots. Many of the *Erica* plants classified as 'erect' showed lateral branches which had equalled or exceeded the original leader in length. Samples from the second year after recolonization showed plants of this kind, and they occur in all subsequent samples, forming the majority of the population in the fourth year. The leading shoot is apparently not superseded so rapidly in *Calluna*, and it is not until the third year after recolonization that samples from the ungrazed plots show bushy plants. Such plants, however, rapidly adopt a dense shrubby form, and by the fourth year most plants are in this condition.

In both species severity of competition is likely to affect this change in growth-form, and may also modify the response to grazing. Further cultural experiments might contribute to the solution of these and related problems, while continued observation of the ungrazed plots will determine whether a change in the habit of *Calluna* may lead to its assumption of dominance. This, however, had not occurred by 1948, 4 years after burning, when a further sampling of the control plots gave figures for air-dry weights of the two species remarkably similar to those of the previous year, viz. *Erica* 23.78 g., *Calluna* 17.14 g. per $\frac{1}{10}$ sq.m. (cf. Table 5).

V. DISCUSSION

In this example of the influence of a biotic factor on the structure of a plant community, it appears that the balance between two dominant plants is directly affected by their morphological responses. Since the dominant plant has a considerable influence on the conditions prevailing in the community, such changes may have widespread implications in community structure. Grazing studies on upland heath which might provide comparisons with the present work are few, and none relates specifically to community structure or the balance between dominants. Boulet (1939) records the following observations on *Calluna* in relation to grazing: '*Calluna vulgaris* seems to have a two-fold character; when closely grazed it can be found in large amount amongst plots having relatively high grazing intensities, but when very little grazed, that is, when rather tall, it is found on plots less frequented by sheep.' This result at first sight appears somewhat at variance with that discussed here. Boulet, however, was not working with a recolonization subsere, and consequently *Calluna* is likely to be naturally dominant in his plots under the lightest grazing intensities, while its abundance under the heavier grazing (which was not over-grazing) is precisely the result described here.

Finally, the significant morphological responses to the removal of the main growing apex by grazing raise interesting physiological problems. The erect form adopted by *Erica* and the bushy form in *Calluna* are perhaps to be expected, but the spreading form of *Calluna* is of particular interest. It would appear that branches from one particular node behave differently from those developing from others. If this behaviour is in any way regulated by growth substances, a most intricate mechanism is likely to be involved.

VI. SUMMARY

The effects of sheep-grazing on the vegetation of a subseral stage in the recolonization of an area of upland heath are analysed experimentally, as an example of the operation of a biotic factor upon community structure. The results are followed by, and interpreted in the light of, laboratory studies on the morphological responses to imitation of grazing in *Erica cinerea* and *Calluna vulgaris*.

(1) The climate, soil and vegetation of the experimental area are described.

(2) An experiment designed to allow investigation of the effect of the intensity of sheep-grazing on the balance between the two dominants (*Erica* and *Calluna*) is outlined.

(3) Re-establishment of these species after severe burning is almost entirely from seed, and seedlings of *Erica* considerably outnumber those of *Calluna*.

(4) The general performance of the two species taken together is shown to be directly related to the intensity of grazing.

(5) In the control plots *Erica* maintains its dominance over *Calluna*.

(6) Grazing at rates between the limits of 50 and 200 sheep-days per plot per year (approx. = not less than one sheep to 4 acres and not more than one sheep to 1 acre throughout a year) shifts the balance in favour of *Calluna*.

(7) At still higher intensities on the severely overgrazed plots it appears that *Calluna* drops out rather more rapidly than *Erica*.

(8) The main features of the early growth morphology of the two species under controlled conditions are compared and illustrated.

(9) Experiments in which the action of the grazing animal is imitated by cutting are described.

(10) Under medium cutting *Erica* produces a few erect branches later supplemented by a small number of additional ones from lower nodes. *Calluna* shows a spreading response, with the development of one to three plagiotropic branches creeping over the soil surface.

(11) Under rather severer treatment, while the response of *Erica* remains unaffected, that of *Calluna* changes to a dense bushy form.

(12) Under very severe treatment both species react alike in the production of a small, more or less dense form.

(13) These responses are explained in terms of the normal behaviour of branches in untreated plants.

(14) An interpretation of the field results on the basis of the greater percentage cover given by the forms produced by *Calluna*, and a reduction in their susceptibility to further grazing is discussed. It is suggested that with the development of these forms *Calluna* gradually obtains a competitive advantage over *Erica*, thus bringing about the change in balance. The similarity of the forms produced by the two species under very severe treatment may account for the retention by *Erica* of the higher proportion in the sparse vegetation of overgrazed plots.

(15) Forms are obtained from the grazed plots of the field experiment which show striking similarity to those produced by imitation of grazing in cultural conditions.

(16) Satisfactory verification of the suggested interpretation is obtained by analysis of the relative proportions of the growth-form types found under the various grazing intensities in the field.

(17) Evidence is given suggesting that, even in the absence of grazing, *Erica* may normally give place to *Calluna* at a later stage in certain areas.

(18) Physiological problems raised by the difference in behaviour of branches from one particular node of a young *Calluna* plant from that of others are mentioned.

(19) The effect of the biotic factor in the locality in which the field experiment was situated is probably to be regarded as an acceleration of seral changes.

The writer wishes to record his indebtedness to Prof. J. R. Matthews for his valuable help at all times; to Dr A. S. Watt for many useful suggestions; to Mr M. H. Quenouille for the statistical examination of Table 7; to the Librarian of the Welsh Plant Breeding Station, Aberystwyth, for the loan of an unpublished thesis; and to Mr I. Moir for taking the photographs.

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THE INTERTIDAL ECOLOGY OF ROCKY SHORES IN SOUTH PEMBROKESHIRE

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(With one Figure in the Text)

I. INTRODUCTION

Previous studies of the littoral (i.e. intertidal) zone of rocky shores in Wales include those of Walton (1915*a, b*) and the writer (Evans, 1947*a*) in Cardigan Bay. One of the most characteristic features of this region is the general poverty and lack of variety among the intertidal fauna; many species which are common on other parts of the coast are occasional only or are totally unrecorded. Walton (1915*a*) listed 156 animal species for both rocky and sandy areas, together with fifty-one species of fish collected by trawling in the bay, while Horsman (1922) adds forty-five littoral species and seventy collected by dredge, grab and trawl from beyond tide marks. I have compiled a list of intertidal and offshore forms from published and unpublished records at the University College of Wales, Aberystwyth, and this comprises 455 species, distributed among the various phyla as shown in Table 1. Many of these records undoubtedly require confirmation, but even if

Table 1. *The marine fauna of Aberystwyth and Bangor*

Phyla	No. of species	
	Aberystwyth	Bangor
Protozoa	2	11
Porifera	5	46
Coelenterata	41	92
Platyhelminthes	13	20
Nematoda	5	2
Nemertini	10	17
Annelida	55	137
Gephyrea	5	8
Arthropoda	147	321
Mollusca	81	234
Bryozoa	19	65
Echinodermata	16	32
Tunicata	5	28
Pisces	51	65
Total	455	1078

all are accepted the list is still a poor one in comparison with that of other localities on the Welsh coast. At the University College of North Wales, Bangor, for instance, records have been made of 1078 animal species for the coasts and adjacent waters (see Table 1). While the more intensive collecting at Bangor may, in part, account for this numerical difference, personal observation has confirmed that localities such as the Menai Straits and the north coast of Anglesey are markedly richer and more varied with regard to their animal populations than the coast of mid-Wales. Many places on the south coast of Wales also have long been recognized as rich collecting grounds for the marine zoologist, and the associations

there met with, in some localities, are very similar to those encountered in the Menai Straits, and again have no counterpart on the barren coasts of Cardiganshire.

It is true that, in Cardigan Bay, certain species, such as barnacles, limpets and winkles, are extremely well represented in numbers, but these are among the hardiest of littoral animals, and more delicate species, such as sponges, anemones, hydroids, ascidians, etc., are very poorly represented. This led to the suggestion of Walton (1915*b*) that the heavy surf action on the exposed west coast of Wales may be responsible for the poverty of the fauna, a suggestion with which the present writer is in full agreement. However, while areas of local shelter from heavy surf are not abundant, they do occur on this coast, but even where the violence of the waves is somewhat abated the littoral associations are by no means as luxuriant as those to be found either in south Pembrokeshire or on the north Wales coast. Moreover, it must be pointed out that wave action on the Welsh coast can only be described as 'relatively violent' in comparison with the world maximal as experienced on the coasts of South Africa, the Pacific coast of North America, etc. Not only is the sheltering effect of Ireland on the west experienced, but the sea floor is fairly shallow, and the full force of Atlantic waves and swells can never reach the Welsh coast. It does not appear that the factor of surf action alone is sufficient to explain the barrenness of the Cardiganshire coast then, and the present study has been undertaken in order to discover what other factors may be held to account for the peculiar features of the shores of Cardigan Bay. A survey has been made of the littoral associations of the south Pembrokeshire coast in the neighbourhood of Tenby. Time did not permit the compilation of anything approaching a complete fauna list, but special attention has been paid to the sponges, anemones, hydroids, polyzoans and ascidians, phyla which are poorly represented in mid-Wales, but which are extremely important constituents of some of the littoral associations both on the coasts of south and north Wales.

It will be convenient here to define my use of the term 'association'. It is not employed in any of the varied but restricted connotations applied by different contemporary ecologists; it is used simply as an alternative to 'community', and means nothing more nor less than an assemblage of plants and animals commonly occurring together under a given set of environmental conditions.

The study is divided into the following sections. A brief account of the geography and geology of the region is followed by a description of climatic and tidal data for Tenby. (This town may be taken as characteristic for south Pembrokeshire as Aberystwyth is taken for Cardigan Bay.) The various zones and associations of the intertidal area are described, and the work ends with a comparison between south Pembrokeshire and the coast of mid-Wales, the possible reasons for differences in the littoral population being discussed.

II. GEOGRAPHY AND GEOLOGY OF THE REGION

Approximately 15 miles of coastline were included in the survey, extending from Manorbier Bay on the west to Telpyn Point on the east (see map, Fig. 1). The area around Old Castle Head, from Precipice Bay to Skrinkle Haven, is inaccessible, since it lies within the bounds of the School of Anti-Aircraft Artillery. On other parts of the coast the cliff face is too precipitous to be negotiated with safety; thus observation in such regions had to be confined to a few selected localities.

Geologically the region may be considered under four different categories: (1) The Old Red Sandstone of Manorbier and Old Castle Head, which passes into (2) the Carboniferous

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Limestone of Lydstep, Giltar Cliffs, the Tenby Peninsula and St Catherine's Island. This is followed by (3) an area of small bays eroded in the Millstone Grits, lying north of Tenby and past Waterwynch Bay, while finally (4) the sea has cut deeply into the Coal Measures to form Saundersfoot Bay, leaving the harder sandstones of Monkstone and Telpyn Point as headlands. Detailed descriptions of the geology of south Pembrokeshire are given by Steers (1946, pp. 162-6), Dixon (1921), Darby (1928) and Leach (1933), while a popular account is presented by the last-named author in his *Handbook to Tenby* (1947).

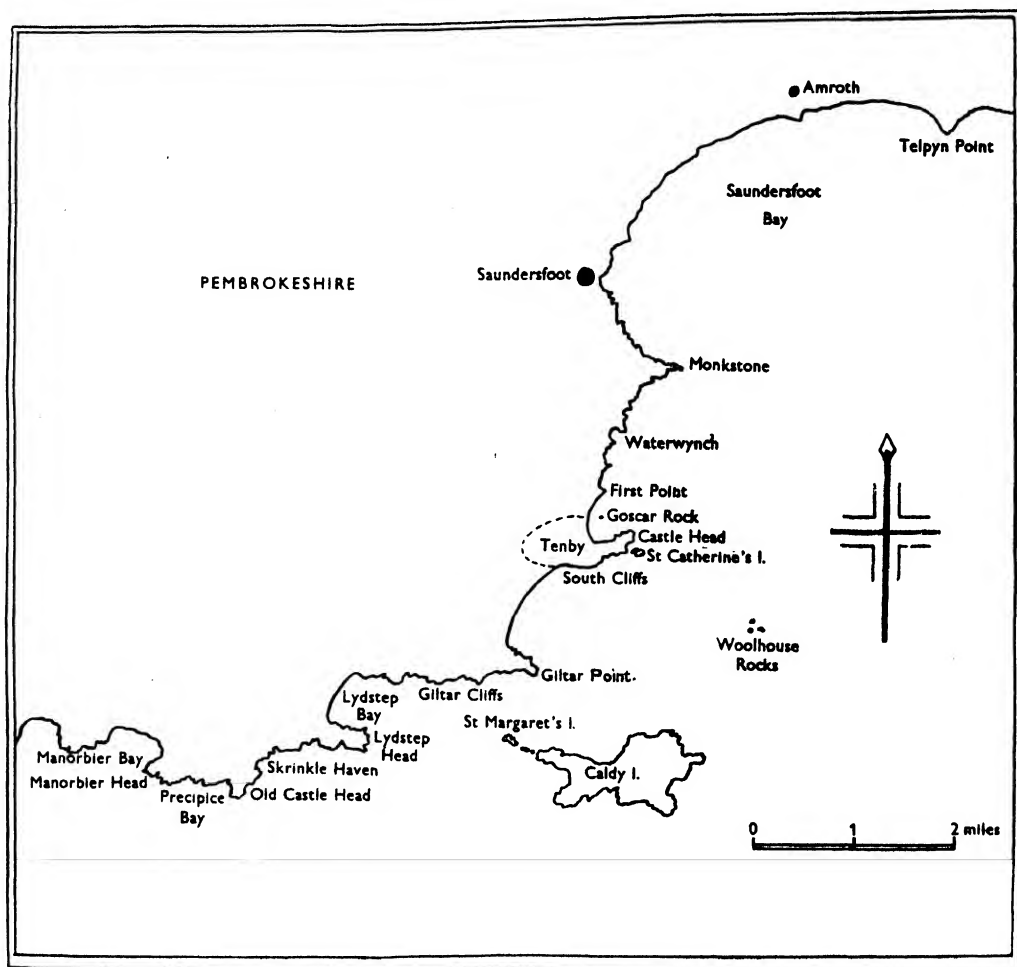


Fig. 1. Map of Pembrokeshire coast, South Wales.

The Old Red Sandstone area includes Manorbier Bay, developed by erosion along groups of small faults in the sandstone strata, and this bay is bounded on the east by Manorbier Headland. The east side of the bay is sandy, but the west side consists of low rocky reefs, striking approximately east and west (i.e. parallel to the sea). The height of these ridges is rarely more than a few feet, but the dip is almost vertical. Loose shingle, sand and gravel occur in gulleys, watercourses, and in the depressions between the parallel reefs, and the shore is backed by low cliffs. On Manorbier Headland the Old Red Sandstone strata are almost vertical, and the shore is steep and narrow. Caves, deep, narrow fissures

and gulleys are developed along small faults, and frequently the shore descends in a series of flat horizontal steps of plateaux to low water. At low water occur reefs and small 'stacks', separated by gulleys and inlets which sometimes contain boulders and loose slabs of rock.

Lydstep Head, Giltar Cliffs, Giltar Point, South Cliffs, St Catherine's Island and Castle Head, Tenby, are formed of Carboniferous Limestone. The cliffs are usually very steep (much steeper than those of Manorbier Headland) or vertical, with numerous narrow caves, steep fissures and caverns, eroded partly by the sea and partly by underground streams (Leach, 1947, p. 70). In many places large slabs and boulders, which have previously broken away from the cliffs, fringe the shore at low water. The limestone itself is often riddled with the burrows of boring animals and pitted with 'solution' hollows. All these holes, fissures, caves, etc., are important in that they provide local shelter from wave crash and direct sunlight.

A small area of Millstone Grits occurs on the east side of Lydstep Head, where the shore takes the form of a raised beach. At the top of the beach there is a flat rocky platform which ends abruptly as a shelf, dropping a few feet vertically to an area of boulders and gravel. (A similar type of raised beach is to be seen on the Carboniferous Limestone of the east side of Giltar Point.) The rest of the Millstone Grit region lies north of Tenby, and black shales and sandstones (e.g. Goscar Rock) appear as outcrops among the grits. From First Point to Waterwynch the coast consists of small bays eroded in the soft shales, separated by headlands of hard, yellow grits. Only at these headlands is rock exposed down to low water, in the bays the lower shore is covered with sand. Caves are not frequent in the Millstone Grits of the headlands, which usually consist of high, jagged reefs, separated by narrow gulleys and inlets.

Farther east the wide bay of Saundersfoot is formed by sea erosion of the Coal Measures, leaving the harder sandstones of Monkstone and Telpyn Point as headlands. Fissures tend to be formed in these headlands by the crushing of softer shales, and Monkstone itself, consisting of two large 'stacks', shows an intermediate stage in the weathering of such headlands, via stacks, into reefs. On the north side of Monkstone there occurs an extensive area of boulders, and it is usual, in Saundersfoot Bay itself, to find the cliff footed by a narrow zone of boulders passing into fine sand.

The whole region is geologically much more varied than the coast of Cardiganshire. The latter consists of Aberystwyth (Silurian) Grits, which tend to weather into small rocky bays separated by short headlands. The softer shales weather away, leaving shallow depressions between low reefs of harder grit, which strike roughly south-west to north-east (i.e. parallel to the coast) and which generally dip towards the land. This type of shore contrasts very strongly with that of the Carboniferous Limestone areas near Tenby. Instead of the cliffs descending almost vertically to low water, the cliff base in Cardigan Bay lies generally in the region of high-water neaps, and below this the beach continues as a series of narrow ledges and reefs as described above. The headlands are short, and any sheltering influence they may exert on the small bays is confined to the upper levels of the beach. Again, quantities of loose drift shingle are characteristic of Cardigan Bay, and this material is constantly in motion under the influence of tidal currents and the prevailing south-westerly winds, scouring and polishing the shore rocks into smooth surfaces. One locality included in the present survey is, however, very similar to the Cardiganshire coast, i.e. Manorbier Bay. Here the reefs (Old Red Sandstone) are steep but not tall, they

strike almost parallel to the sea, and there is marked evidence of abrasion by moving shingle. Elsewhere (i.e. farther east) conditions are very dissimilar, both in rock formation and in the absence of shingle. The only part comparable in rock configuration with Cardigan Bay then is Manorbier Bay, and it will be seen later that this is the only locality included in the survey which is similar to Cardigan Bay with regard to its intertidal associations.

III. TIDAL DATA, CLIMATE, AND EXPOSURE TO SURF

Tidal data

These are obtained from *Admiralty Tide Tables* (1948), Section A, Parts I and II. The nearest Standard Port is Pembroke Dock, and a tidal scale for Tenby has been constructed by making adequate corrections. This scale is given in Table 2. Extreme high- and low-water springs and neaps are heights for 1948, and all levels are expressed as feet above or below Chart Datum.

Table 2. *Tidal scales at Aberystwyth and Tenby*

	Aberystwyth	Tenby
E.H.W.S.	+ 15.3'	+ 28.7'
M.H.W.S.	+ 13.9'	+ 25.9'
M.H.W.N.	+ 10.8'	+ 19.2'
E.H.W.N.	+ 9.9'	+ 16.8'
M.T.L.	+ 7.2'	+ 13.2'
O.D.	+ 7.1'	+ 12.8'
E.L.W.N.	+ 5.3'	+ 10.1'
M.L.W.N.	+ 3.7'	+ 7.8'
M.L.W.S.	+ 0.2'	+ 1.0'
C.D.	0	0
E.L.W.S.	- 1.4'	- 2.2'

Note. Extreme springs and neaps for Aberystwyth are mean values for the period 1937-46, those for Tenby are 1948 values.

The tidal range at extreme springs is 30-31 ft., and at extreme neaps it is 6-7 ft., in comparison with springs of 16-17 ft. and neaps of 4-5 ft. at Aberystwyth. It is unlikely, however, that this factor in itself can exert a direct influence in the intertidal population, except to modify the width of the various zones on the shore.

The period of the day at which low water of springs occurs is likely to be important to animals which inhabit the lowest levels on the shore. At Tenby low springs occur in the early afternoon, and at Aberystwyth an hour or two later. This is unfavourable to the fauna at both places, but it must be noted that in south Pembrokeshire the presence of caves, fissures, overhangs, etc., provides adequate shelter from direct sunlight for many species characteristic of the lower part of the littoral zone. In Cardigan Bay, however, the rock configuration does not generally provide such shelter.

Climate

Meteorological data supplied by the Borough Accountant for Tenby include mean maximum and minimum monthly temperatures, the monthly average of rainfall (inches), and the monthly total of sunshine hours. These may be compared with similar data for Aberystwyth supplied by the Harbour Master (Table 3). All data are for the year 1947.

It is obvious from these two sets of figures that there is little difference between the climate of south Pembrokeshire and that of Cardigan Bay. The maximum range of tempera-

ture does not much exceed 45° F. at either place, which is not excessive. Even in summer the highest recorded temperatures during 1947 were only 85·0° F. (Tenby) and 84·0° F. (Aberystwyth), and the lowest minimum was 19° F. for both places. The climate is typically northern cold temperate, and typical of the south-west coasts of the British Isles.

Clearly no differences in the climate of the two coasts are of sufficient magnitude to explain the dissimilarity of the littoral populations.

Table 3. *Climatic data for Aberystwyth and Tenby*

	Mean max. ° F.		Mean min. ° F.		Total rainfall		Total sunshine (hr.)	
Month	Tenby	Aberystwyth	Tenby	Aberystwyth	Tenby	Aberystwyth	Tenby	Aberystwyth
Jan.	43·9	44·0	35·6	35·1	5·83	2·87	54·6	66·8
Feb.	35·2	35·0	28·8	28·0	3·52	0·15	37·9	64·1
Mar.	44·5	46·0	35·7	35·5	9·61	5·53	80·6	78·0
Apr.	52·0	52·4	42·4	43·0	3·43	1·76	149·7	143·5
May	58·9	61·2	47·7	48·6	2·89	2·97	191·6	176·7
June	63·0	65·8	52·1	53·0	3·7	1·97	165·9	151·3
July	65·6	65·6	56·2	55·5	4·06	5·21	164·8	141·1
Aug.	74·0	74·8	58·2	59·2	0·84	0·47	300·0	312·9
Sept.	65·0	65·7	53·5	55·0	2·68	2·29	131·9	148·0
Oct.	58·8	?	48·5	?	1·34	?	130·7	?
Nov.	52·1	?	43·2	?	4·81	?	57·2	?
Dec.	48·0	45·1	39·7	40·0	4·64	3·65	34·6	26·7

Exposure to surf

Details of wind direction and strength were not available at Tenby, but several observers confirm the assumption that prevailing winds are from a westerly and south-westerly direction, and that gales from the east are occasional. This is also true of Aberystwyth (Evans, 1947*a*, fig. 3). The set of the tides is from the west, and the net result is that exposure is largely from the south and west.

From the point of view of exposure to waves the region studied may be divided into three quite distinct areas (see Fig. 1):

(a) Manorbier Bay to Lydstep Head is open from the south-west to the east. Even on the south-west the nearest sheltering influence, St Govan's Head, is about 5 miles distant, and the area may be described as 'very exposed'. Local shelter is experienced, however, in caves and fissures, etc., and on the north-west side of Manorbier Headland.

(b) Lydstep Bay to Giltar Point, like the previous region, faces due south and is open to winds from this quarter, except where the sheltering influence of St Margaret's Island and the western extremity of Caldy Island is experienced. The region is sheltered from the south-west by Lydstep Head, and from the south-east by Caldy Island, and is consequently much less exposed to heavy wave action than is the Manorbier to Lydstep region. Again local mitigation of the adverse effects of surf is experienced in the numerous caves and fissures, while the jumbled mass of rocks common at the foot of the cliffs also exert some sheltering influence on the lower part of the intertidal zone.

(c) The coast from Giltar Point to Amroth faces in a general easterly direction; thus it is not open to westerly exposure. Caldy Island lies due south, and the stretch is, as a whole, far less exposed than either of the other two regions. The chief exposure is experienced on the south flanks of headlands such as Monkstone and Telpyn Point.

From the point of view of surf exposure as from that of rock configuration, again the only part of the region at all comparable with the exposed shores of Cardigan Bay is the stretch from Manorbier Bay to Lydstep. Even here the shore is sheltered to the north and

west, while Cardigan Bay is open to these quarters, and positions of local shelter are much more frequent (especially in the Carboniferous Limestone of Lydstep) than they are on the coasts of mid-Wales.

IV. THE LITTORAL ASSOCIATIONS

It is proposed to adopt the suggestion made by Stephenson (1939) and followed by subsequent workers that the region between tide marks be divided into three zones, i.e. the 'Littorina', 'Balanoid' and 'Laminarian' zones. There is considerable evidence to suggest that this type of zonation is a basic pattern which may, in response to variations in local factors, be subjected to different types and degrees of modification. This I have previously shown both on the coast of mid-Wales (Evans, 1947*a*) and on the south coast of Devon (Evans, 1947*b*), and the same is true in south Pembrokeshire. The modifying factors are, as usual, chiefly those of surf and wave action, correlated with variations in rock configuration, geographical aspect, texture of the substratum, and the presence or absence of loose material in the form of gravel, sand or pebbles.

A. *The Littorina zone*

A zone dominated by *Littorina neritoides* (L.) and *L. rudis* (Maton) and restricted to the higher levels of the shore, this is generally better represented on the coast of south Pembrokeshire than it is in Cardigan Bay. In the latter region the cliff face is frequently totally devoid of *Littorina*, since it lies above the region of tidal influence, and the higher levels of the littoral zone are occupied by a beach of drift shingle. The steep cliffs descending almost vertically to low water, typical of south Pembrokeshire, are, however, eminently suited to these two species. At exposed points such as Lydstep Head, Giltar Cliffs, Monkstone Point, etc., where splash and spray are thrown up to considerable heights, both species are particularly numerous, and the zone may extend as high as 30 ft. above high-water mark. On sheltered faces, e.g. in caves, and on the north side of Castle Head, Tenby, the absence of splash and spray does not favour a densely populated *Littorina* zone.

As usual *L. neritoides* prefers somewhat more exposed conditions than does *L. rudis*, and the latter favours rougher and more fissured rock (e.g. the flat tops of rocks at Manorbier Headland). Both species persist down into the zone dominated by barnacles; I have taken *L. neritoides* occasionally as low as M.T.L. in south Pembrokeshire, as in Devon (Evans, 1947*b*), and *L. rudis* even lower than this. *L. rudis* is also characteristic of the upper Balanoid zone.

Together with the two molluscs, other animals may be regarded as typical of the *Littorina* zone. *Ligia oceanica* (L.) and *Petrobius maritimus* Leach are frequently common above high-water mark, particularly in the dark cracks and crevices in limestone rocks. Both are occasional only in Cardigan Bay, a fact which is probably related to the absence of suitably fissured strata. The harpactid *Tigriopus fulvus* (Fischer) occurs in pools in this zone; *Lipura maritima* Guerin is common both on the surface film of such pools and on damp rock. The centipede *Geophilus maritimus* Leach and an unidentified species of *Lineus* are to be found in dark crevices. Some species more characteristic of the Balanoid zone below also succeed in penetrating for a short distance into the zone of *Littorinas*. Thus spots of *Chthamalus stellatus* (Poli) occur above the usually well-marked 'barnacle-line' which marks the upper limit of barnacle dominance. *Patella vulgata* (L.) succeeds in reaching levels above M.H.W.N. only in shady cracks and on north-facing overhangs. This

may be related to the general southward orientation of the coast (Orton, 1929), for on the west-facing shores of Cardigan Bay limpets are fairly common in the lower part of the *Littorina* zone even on open rock (Evans, 1947c).

The flora of the *Littorina* zone is poor from the point of view of variety of species, and consists mainly of certain species of lichens, e.g. the so-called 'orange lichens' of the genus *Xanthoria*, branched green lichens such as *Ramalina* spp., and *Verrucaria* spp. These latter frequently form a distinct black paint-like band along the rock just above the 'barnacle-line'. *Lichina confinis* Ag. occurs under very exposed conditions (e.g. at Manorbier Headland), but the allied species *L. pygmaea* Ag., which occurs below it, seems to be slightly less demanding of surf. This species often forms a very distinct band of scrubby growth along the cliff face, visible from some distance away, lying partly in the *Littorina* zone and partly in the *Balanoid* zone. Naylor (1930) has suggested that *L. pygmaea* is restricted to south-facing shores in the neighbourhood of Plymouth, but I have found it growing quite luxuriantly on north-facing overhangs and in damp and shady fissures as well as on exposed south-facing slopes, and this both in Cardigan Bay and in south Devon (Evans, 1947a, b). The same is true of the lichen in south Pembrokeshire. Thus on the very sheltered north side of St Catherine's Island *L. pygmaea* is very thick and much more extensive than it is on the south and west of the same island. Naylor (1930) suggests that the lichen requires a certain amount of drying out from time to time, hence its restriction to well-lit south faces. This suggestion is not, however, compatible with its habit of growing in damp shady cracks, as both Rees (1935) and I have described, and I venture to suggest that the opposite is true, i.e. that *L. pygmaea* is intolerant of desiccation. This would explain, first, its restriction to shady faces and damp crevices at sheltered localities (e.g. St Catherine's Island) where, even if it occurred on the more exposed south or west faces, it would receive but little splash; and secondly, the fact that it occurs on sunlit south faces only where heavy surf is experienced and splash and spray are frequent, so avoiding long periods of drought.

The only algal representative at all common in the *Littorina* zone is *Enteromorpha compressa* Grev., and this is restricted to areas where fresh water percolates through the cliff face. Even permanent rock pools at such high levels are generally devoid of any conspicuous flora unless the cliff face is exposed to exceptionally strong surf, in which case encrusting algae of the 'lithothamnion' type may coat the floor of the pool with a thin crust.

B. The *Balanoid* zone

This is the widest zone on the shore, extending under optimum conditions almost from m.h.w.s. to m.l.w.s. It is also the zone most subject to modification in response to local factors of rock configuration, surf, etc. It is proposed, first of all, to consider the zone in its simplest form, then to describe the modifications which are met with in the region covered by the present survey. Some of these are more or less common to all coasts and I have commented upon them previously (1947a, b), others are more local in their appearance and will be dealt with in correspondingly greater detail.

(1) *Basic form*

In its simplest form the *Balanoid* zone, on the south-west coasts of England (see Moore & Kitching, 1939), may be divided into two subzones, both of which are characterized by barnacles. There is an upper or 'Chthamalus subzone' dominated by *Chthamalus stellatus* (Poli) and a lower or 'Balanoides subzone' dominated by *Balanus balanoides* (L.).

Along most of the south Pembrokeshire coast the cliff face is steep or vertical, and the upper limit of the Balanoid zone is well marked as a 'barnacle-line', which is recognizable even at a distance, especially on limestone areas (e.g. Caldy Island, Giltar Cliffs, etc.). Above this line *Chthamalus stellatus* occurs as small patches and isolated individuals, but the line marks the beginning of barnacle dominance and hence the top of the Balanoid zone. It varies in height between M.H.W.S. and M.H.W.N. according to the degree of surf action and the amount of splash, as I have shown previously. In Cardigan Bay, where the Balanoid zone is often to be seen in its simplest form, there is commonly a well-marked 'lower barnacle-line', separating off the zone of barnacles from that of the laminarians, but this is much less frequently seen in south Pembrokeshire owing to the fact that the lower part of the Balanoides subzone is so often invaded by other communities. On the vertical, seaward, exposed faces of stacks and reefs at Manorbier and Lydstep, however, the Balanoid zone may pass abruptly into a belt of rock colonized only by encrusting algae, and here the 'lower barnacle-line' may be distinguished at a height of approximately M.L.W.S. + 1 ft., which is comparable with its height in Cardigan Bay. The height at which the *Chthamalus* subzone passes into the Balanoides subzone is, as I have remarked elsewhere, extremely variable, but seems to be related in some way to the amount of shelter from surf which is experienced. *C. stellatus* appears to be far less tolerant of shelter than is *Balanus balanoides*; moreover, in caves and caverns (e.g. St Catherine's Island) where the latter barnacle is often very thickly distributed as insecurely attached but very tall (over 2 cm.) individuals, *Chthamalus* is usually totally absent. It seems that *Chthamalus*, unlike *Balanus balanoides*, is unable to compensate for lack of wave crash by utilizing strong currents and wash (Fischer-Piette, 1929, 1936; Moore, 1935; Hatton, 1938). However, where the Balanoid zone is in its simplest form both subzones are represented. Such localities are those most open to wind and surf, e.g. vertical stacks at Manorbier and Lydstep Heads, the seaward extremity of Monkstone Point, etc., and here the complete zonal pattern is Littorina zone, *Chthamalus* subzone, Balanoides subzone, and Laminarian zone.

At such localities, although barnacles are thickly crowded on the rocks and the zone is well populated with individuals of a few species, there is little species variety. Certain species are, however, more or less characteristic. *Lichina pygmaea*, *Littorina neritoides* and *L. rudis* extend down from the Littorina zone, while other species are more characteristic of the Balanoid zone itself. Limpets are numerous throughout, though never very large, probably due to the intense competition for space to which they are subjected by the barnacles (Hatton, 1938). *Patella vulgata* L. and *P. depressa* Pennant are characteristic, while *P. athletica* Bean inhabits damp cracks and 'clean' lithothamnion-encrusted pools. *Mytilus edulis* L. occurs in the middle and lower regions of the Balanoid zone, but the individuals are never large in size unless sheltered to some degree from the full violence of the waves. Mussels usually congregate in hollows on exposed faces, which seems to suggest that they encounter more difficulty in settling and hanging on than do the barnacles. Where the rock is calcareous *Hiatella arctica* (L.) burrows freely in the lower part of the Balanoid zone, so does the polychaete worm *Polydora ciliata* (Johnston). *Nucella lapillus* (L.) is restricted to the local shelter of cracks and hollows, but in caves where the walls are thickly encrusted with *Balanus balanoides* hundreds of *Nucellas* may be found hanging on to these vertical walls. The anemone, *Actinia equina* L., appears to be fairly tolerant of surf and occurs in the Balanoid zone of exposed localities, while *Eulalia viridis* (O. F. Müller), *Lineus ruber* (Müller), and *Geophilus maritimus* may be found crawling among

the barnacles. Sponges such as *Hymeniacidon sanguinea* (Grant) and *Halichondria panicea* (Pallas) occur as thin crusts in crevices, but none of the more delicate sponges is found, while the only algae which are typically present are lithothamnium.

This, then, is the fundamental form of the Balanoid zone; an association dominated by barnacles, but with very little else except a few hardy and robust species such as limpets, species which can temporarily retreat from surf (e.g. *Eulalia*, *Lineus* and *Actinia*), or species whose growth habit enables them to withstand wave-shock (e.g. encrusting algae and sponges).

(2) *Invasion by fucoid algae*

Under conditions of shelter from surf the Balanoid zone becomes invaded by fucoid algae, and the extent to which this invasion and consequent obliteration of the basic zonal pattern is carried, is directly proportional to the amount of shelter experienced. In extreme cases the entire zone of barnacles is obscured by a growth of *Pelvetia canaliculata* Decne & Thurs., *Fucus spiralis* L., *Ascophyllum nodosum* Le Jol. and/or *Fucus vesiculosus* L. and *F. serratus* L., in that order proceeding down the shore. Only in one locality in the present survey was this full development of the algal series observed, i.e. on a small area on the very sheltered north side of Castle Head, Tenby. Here *Chthamalus* is entirely absent, and *Balanus balanoides* occurs only in small patches beneath the algae. Generally speaking, much of the south Pembrokeshire coast is composed of very steep cliff faces, and though these may receive shelter from the prevailing winds, steep faces are only colonized with difficulty by algae. It is interesting to note that the Old Red Sandstone of Manorbier, though less sheltered from wind and surf than the limestone cliffs farther east, often carries a better algal cover than these cliffs. This is related to the more broken nature of the shore, the presence of horizontal platforms of rock, etc., on which algal spores can settle and become established much more easily than they can on steep or vertical limestone faces, although the latter may be less exposed to prevailing winds and surf action.

Intermediate stages between a purely Balanoid and a purely Fucoid type of zonation are extremely common, and the proportion of barnacles and weeds on such mixed Balanoid-Fucoid shores is, as usual, determined by factors of surf action and rock slope. I have commented on such communities elsewhere (Evans, 1947*b*), and the suggestions and conclusions are substantiated by observation during the present survey.

Together with the reduction of wave crash and the invasion by brown algae, other organisms make their appearance in the mixed barnacle-weed communities. *Nucella lapillus* becomes less restricted to the local shelter of crevices and hollows, *Mytilus edulis* is normally more widespread and the individuals are larger in size, *Littorina littorea* (L.) appears in numbers, and *L. littoralis* (L.) occurs on the clumps of weed. Two gastropods commonly associated with mixed barnacle and fucoid communities in Cardigan Bay are, curiously enough, much more local in their distribution in south Pembrokeshire. These are *Gibbula umbilicalis* (da Costa) and *Osilinus lineatus* (da Costa). During the survey they were found in numbers only in Manorbier Bay and on the boulder beach to the north of Lydstep Head, although the type of ground they seem to favour (i.e. a level shore with broken rock, boulders and shallow pools) is common at several other localities. *Gibbula cineraria* (L.) occurs at lower levels in the Balanoid zone and in the Laminarian zone almost everywhere; indeed, it is far more common on this coast than it is in Cardigan Bay. Moreover, it extends well above M.L.W.N., which is its upper limit of distribution in the

latter region. Walton's (1915*a, b*) survey of the Cardiganshire coast revealed the absence of these Trochidae in the centre of the Bay, and he suggested that the snails shunned areas of lime-free drainage. At the present time, however, all three species have spread northward in the Bay and are common even in lime-free areas. This fact, together with the infrequent occurrence of two of the snails on the south Pembrokeshire limestone coasts and their abundance on areas of Old Red Sandstone, would suggest that some other explanation must be sought for their curiously local distribution.

Sabellaria alveolata (L.) also presents a problem of local distribution. In Cardigan Bay it is widespread in semi-exposed and sheltered conditions, but in the area in the immediate vicinity of Tenby and from here to the west the species is absent, although its obvious requirements (i.e. shelter, flat rocks, shallow pools, sand for tube-building) are frequently met with. Yet a short distance away to the east, in Saundersfoot Bay, *Sabellaria* forms extensive cushions and sheet-like colonies on the mid-tidal rocks as it does in mid-Wales. At Tenby (e.g. on St Catherine's Island) another tubiculous polychaete, i.e. *Polydora ciliata*, seems to occupy the *Sabellaria* 'niche'. This worm bores into the calcareous rock, lining its burrows with tubes of mud which protrude above the rock surface and, especially in very sheltered localities, form banks of tubes on the surface just as *Sabellaria* does, except that the tubes are much more delicate and smaller.

(3) *Balanus perforatus* and *Fucus serratus* subzones

I have described previously (p. 125) how the jumbled mass of broken rock at the foot of the limestone cliffs in many localities creates an area of local shelter from surf at lower shore levels. Here, although the basic zonal sequence of Littorina zone, Chthamalus subzone and Balanoides subzone is present in its simplest form on the vertical cliff faces, the lower part of the Balanoides subzone is affected by the presence of these sheltering rock masses. Two very definite types of association can be distinguished: (a) an association characteristic of the seaward faces of the loose rock slabs, exposed both to waves and to direct illumination, and (b) a cryptofaunal association developed on the landward, sheltered and shady overhangs of the same loose rocks. This latter type of association will be considered later (p. 131).

On the south, west and east faces of these slabs, and on the cliff face behind them, *Balanus balanoides* does not extend thickly to the Laminarian zone as it does under more exposed conditions. The slight increase in shelter allows the development of another barnacle, *B. perforatus* Bruguière, a species which is characteristic of local shelter at exposed localities and which favours strong water movement but not pounding surf (Fischer-Piette, 1936). It occurs in much the same type of situation in south Devon and Cornwall (Evans, 1947*b*), but is absent from Cardigan Bay. Often *B. perforatus* is dense enough to constitute what may be termed a *B. perforatus* subzone, and with it are frequently associated masses of small 'seed' mussels and the weed *Laurencia pinnatifida* Lamour. This weed and the barnacle appear to have similar optimum requirements of surf, not only in south Pembrokeshire but also elsewhere. Conditions are usually still too rough for *Fucus serratus* in this *Balanus perforatus* subzone, but lower down, as the influence of the sheltering rock masses tends to become more effective, this alga begins to appear, and it is usual for the subzone to pass into a *Fucus serratus* subzone before the Laminarian zone is reached. Levels occupied by this *Balanus perforatus* subzone of south Pembrokeshire are often occupied by coralline algae (e.g. *Corallina squamata* Ellis) in Cardigan Bay, and the

same is true in Manorbier Bay where *Balanus perforatus* is again absent or poorly developed. Thus it seems that the *Balanus perforatus*-*Laurencia pinnatifida* community is equivalent to the *Balanus balanoides*-*Corallina squamata* community of slightly more exposed localities.

Passing down into the *Fucus serratus* subzone *Laurencia* continues to be fairly common, while *Chondrus crispus* Lyngb., *Lomentaria articulata* Lyngb., *Ulva lactuca* Linn., *Enteromorpha* sp., *Rhodomenia palmata* Grev., *Ceramium rubrum* C. A. Agardh, and *Chaetomorpha crassa* Kütz are characteristic species of the under-flora. *Balanus balanoides* and *B. perforatus* occur in thin patches, *Nucella lapillus* is present but is not as common as it is higher up, masses of small *Mytilus edulis* occur, and either *Polydora ciliata* or *Sabellaria alveolata* form sheets of tubes over the rock. *Hiatella arctica* and the sponge *Cliona celata* Grant commonly bore into calcareous rocks at such levels, while *Hymeniacidon sanguinea* and *Halichondria panicea* occur in the form of thin sheets. *Pomatoceros triqueter* (L.) and *Filograna implexa* (Berkeley) frequently build their tubes on the rock surface, while *Eulalia viridis* commonly crawls among the weed. *Littorina littoralis* clusters on the fucoids, while *Patella vulgata* and *P. athletica* may be found beneath. *P. depressa*, preferring more surf-beaten localities (Evans, 1947c), is normally absent. Although this *Fucus serratus* subzone possesses a fairly varied population, the actual rock face is never thickly covered, and it is noticeable that the species are all comparatively hardy ones, and able to withstand a fair degree of surf action. The association is very similar to the *F. serratus* association of the Cardiganshire coast, and this is especially true in Manorbier Bay, where *Balanus perforatus* is absent as it is in mid-Wales.

(4) The 'cryptofaunal' community

The shaded, sheltered and overhanging faces of the rock masses at the cliff base carry an entirely different association from the more exposed, seaward, well-illuminated faces. Not only is this association to be seen on the overhangs of such rocks, but it is also developed, to a lesser extent, on north-facing slopes generally (e.g. the north faces of St Catherine's Island, Monkstone, etc.), and in quiet caves and fissures, all along the coast, except in the region Manorbier to Lydstep Head. Since it appears to be intimately associated with shade, and since it is difficult to pick out any one or two dominant species, I have called this association the 'cryptofaunal community'. It should be noticed, however, that deep shade alone is not the only requisite of this community. Thus on Manorbier Headland, although north-facing surfaces and overhangs, deep caves and fissures, etc., are common, the association is not encountered. On the west side of this headland, however, as the cliffs turn to face the north-west (see Fig. 1) and become more sheltered, the association begins to appear. Similarly at Lydstep, where the sheltering influence of Old Castle Head is experienced, again the community may be seen under overhangs. It would appear from this that, although positions of local shelter are to be found on Manorbier Headland itself, what we might call the 'over-all' exposure of this particular part of the coast is too great to allow of the development of the species which constitute the cryptofaunal community.

It is quite obvious at first sight that this is the richest association on the shore. Time did not allow very extensive collection and identification of the species which enter into its formation, but certain species are extremely common, and mention of these will be sufficient to demonstrate how rich and varied is the association. *Lomentaria articulata* appears to be the dominant alga and this together with various sponges, hydroids and ascidians, forms a thick spongy mat over the whole rock surface, except at the openings to the burrows of

Hiatella arctica which riddle the rock when this is of a calcareous nature. Barnacles and limpets, which are so typical of the open faces, are almost completely absent except where an occasional patch of bare rock occurs, and it seems clear that they are excluded from the community by the lack of suitable settling space rather than by any other factor. The weeds typical of the *Fucus serratus* subzone (see p. 130) occur, except that the fucoid itself is occasional only and *Laminaria digitata* Lamour is present as isolated plants. In general the Rhodophyceae are much better represented than either the Chlorophyceae or the Phaeophyceae, and this is presumably due to the low intensity of light, for in the darkest overhangs and caves practically only red algae survive.

Together with *Hiatella arctica*, *Polydora ciliata* also bores the rock and its tubes often form a layer on the surface. Sponges such as *Halichondria panicea*, *Hymeniacidon sanguinea*, *H. caruncula* Bowerbank and *Myxilla incrustans* (Johnston) aid in the formation of the mat, and form thick fleshy cushions, very different from the thin encrusting sheets which is their habit of growth in more exposed places in south Pembrokeshire and which is their usual habit in Cardigan Bay. Other sponges characteristic of the community, but not actually taking part in the formation of the mat, are *Grantia compressa* (Fabricius), *Sycon coronatum* (Ellis & Solander), and *Leucosolenia botryoides* (Ellis & Solander), the last species usually growing around the stems of fucoids and laminarians. These last three sponges require appreciably more shelter than the encrusting types; in Manorbier Bay, for example, they are occasional only, as they are in Cardigan Bay, while encrusting species may be well represented even if they do occur only as thin sheets. Finally, *Cliona celata* bores into the rock and is visible as small orange pustules among the matted growth.

Hydroids are extremely well developed both in the mat itself and on the algal thalli. The following species have been collected and recorded:

Aglaophenia pluma (L.), *Calycella syringa* (L.), *Clava multicornis* (Forskål), *Clytia johnstoni* (Alder), *Coryne muscoides* (L.), *Diphasia rosacea* (L.), *Dynamena* (*Sertularia*) *pumila* (L.), *Eudendrium ramosum* (L.), *Halecium* sp., *Kirchenpaueria* (*Plumularia*) *pinnata* (L.), *Laomedea* (*Campanularia*) *flexuosa* Hincks, L. (*Campanularia*) *neglecta* Alder, *Obelia dichotoma* (L.), *O. geniculata* (L.), *Plumularia setacea* (Ellis & Solander), *Sertularella polyzonias* (L.), *S. rugosa* Gray, *Sertularia operculata* L., *Stauridium productum* Wright, *Tubularia indivisa* L., *T. larynx* Ellis & Solander, and *Turris neglecta* Lesson (see Hincks, 1868). Some of these species grow on the rock itself, some on other hydroids, on sponges and on *Fucus* and *Laminaria*. Together they form an important constituent of the cryptofaunal community.

Among the more conspicuous elements of the fauna of the shady, protected overhangs are the anemones. Many of these also occur in other situations, e.g. in dark shaded pools in the caves and caverns of Lydstep Head, St Catherine's Island, etc., but it is amongst the cryptofaunal population that they achieve their best development. Most of them require a great deal of shelter both from surf and direct illumination, and it is quite noticeable that they are not as numerous or as large on vertical rocks facing north, however shady these may be, as they are on more sheltered overhangs. Their habit of affixing themselves in cracks, crevices, empty *Hiatella* burrows, etc., may also be important with respect to water movement, and at low tide such anemones may be observed hanging down as long finger-like processes which, at the slightest touch, will contract rapidly into their holes or cracks. *Actinia equina* L. is, as usual, very abundant and widespread, being the most tolerant of the actinians with regard to surf and exposure to air. Thus it is to be found up

in the middle of the Balanoid zone, whenever a projecting rocky ledge or shelf offers the slightest amount of shelter from wave crash, and it is abundant under the exposed conditions prevalent in Manorbier Bay, where other anemones are absent. *Sagartia elegans* (Dalyell), though much more restricted in its distribution, is also extremely common in the cryptofaunal association, especially var. *nivea* (Gosse) and var. *venusta* (Gosse). The var. *miniata* (Gosse) is somewhat less common, while var. *rosea* (Gosse), with its beautifully coloured magenta tentacles, was taken only in sheltered and shady rock pools at Lydstep. *S. troglodytes* (Price) var. *decorata* occurs not only under overhangs and in caves but also in gravel and on the under-surface of loose stones. *Actinothoe sphyrodeta* (Gosse) is another common inhabitant of the cryptofauna. *Metridium senile* (L.) var. *dianthus* (Ellis) is found both in pools and on overhanging surfaces, but individuals in the latter habitat are never very large compared with the specimens to be seen in shady pools. *Tealia felina* (L.) var. *coriacea* (Cuvier) is even more restricted to pools and to the under-side of stones set in sandy gravel; it does not appear to favour the pendant habit. These anemones seem to be best developed on limestone rocks, possibly due to the abundance of *Hiatella* burrows, and are generally poor on Old Red Sandstone areas.

A varied population of bryozoans occurs in the cryptofaunal community, growing on algae, hydroids, sponges and on the rock itself. Species collected and identified include the following: *Aetea anguina* (L.), *Alcyonidium gelatinosum* (L.), *A. hirsutum* (Fleming), *Amathia lendigera* (L.), *Bicellaria ciliata* (L.), *Bowerbankia imbricata* (Adams), *Bugula flabellata* J. E. Gray, *B. turbinata* Alder, *Chorizopora brongniartii* (Audouin), *Cribrilina radiata* (Möll.), *C. punctata* (Hassall), *Crisia denticulata* (Lamarck), *C. eburnea* (L.), *Eucratea chelata* (L.), *Flustrella hispida* (Fabricius), *Lepralia pallasiana* (Möll.), *L. pertusa* (Esper), *Membranipora flemingi* Busk, *M. lineata* (L.), *M. membranacea* (L.), *M. pilosa* (L.), *Membraniporella nitida* (Johnston), *Mucronella coccinea* (Abildgaard), *M. peachii* (Johnston), *Pedicellina* sp., *Schizoporella linearis* (Hassall), *S. unicornis* (Johnston), *Scrupocellaria scruposa* (L.), *S. reptans* (L.), *Valkeria uva* (L.).

Only nineteen species of Bryozoa have, as yet, been recorded in Cardigan Bay, and this includes both littoral species and those taken in the trawl and dredge. The list above, comprising thirty species, is by no means an exhaustive one, and points to the fact that the bryozoan population (like that of the sponges, anemones and hydroids) of south Pembrokeshire is far richer than that of the coast of mid-Wales.

As prominent in the cryptofaunal association as the sponges and anemones are the ascidians. Both solitary and compound forms occur, the latter as brightly coloured, fleshy cushions among the matted growth on the rock surface, the yellow colonies of *Amaroucium*, the orange growths of *Morchellium* and the brick-red clusters of *Dendrodoa grossularia* being especially noticeable. The following ascidians were collected and identified: *Amaroucium punctum* Giard, *Ascidia mentula* O. F. Müller, *Ascidella scabra* (O. F. Müller), *Botrylloides leachii* Savigny, *Botryllus schlosseri* (Pallas), *Clavelina lepadiformis* (O. F. Müller), *Corella parallelogramma* (O. F. Müller), *Dendrodoa grossularia* (van Beneden), *Didemnum gelatinosum* Milne Edwards, *D. maculosum* Milne Edwards, *Molgula* sp., *Morchellium argus* (Milne Edwards), *Polyclinum aurantium* Milne Edwards, *Sidnyum turbinatum* Savigny, *Styela* sp. (*coriacea*?), *Trididemnum tenerum* (Verrill), comprising a total of seventeen species. Only five ascidians have, as yet, been recorded in Cardigan Bay.

Another conspicuous inhabitant of shady and protected situations is the alcyonarian *Alcyonium digitatum* L. This occurs very low down in the Balanoid zone and in the

Laminarian zone, but is often extremely well developed and fairly common. Crawling over the matted weeds, hydroids, etc., *Eulalia viridis* occurs in considerable numbers, while *Aeolidia papillosa* (L.) has been observed feeding on the rich population of anemones. Molluscs such as *Nucella* and *Littorina* are only occasional, and do not appear to be characteristic inhabitants of this particular type of environment. At some localities the white tubes of serpulid worms are a conspicuous feature, especially on some north-facing cliffs, where the base of the rock tends to be covered with silt (e.g. the north face of St Catherine's Island).

The cryptofaunal community is then, with the possible exception of the Laminarian zone, the richest association between tide marks. It is developed in response to local conditions (i.e. the presence of overhangs and caves low down on the shore) and has no counterpart whatsoever on the shores of Cardigan Bay.

(5) *Invasion of the Balanoid zone by mussels*

One modification of the Balanoid zone which appears to be very common on the south Pembrokeshire coasts is the invasion of the zone by *Mytilus edulis*. This is particularly characteristic of boulder areas (e.g. on the north side of Monkstone), and of low-lying rocky reefs on sandy beaches (e.g. Saundersfoot Bay). Extensive beds of mussels occur, and *Balanus balanoides* is restricted to the occasional patches of bare rock or stones or to the shells of the mussels themselves. In such areas *Littorina littorea* is also common, and the mid-beach is occupied by what might be termed a *Balanus-Mytilus-Littorina* community. Limpets are occasional only; they must find great difficulty in settling in such an area, where competition for space is obviously very intense. *Nucella* is usually fairly common, and so is *Actinia equina*. The chief weeds are isolated clumps of *Fucus vesiculosus* and, lower down, *F. serratus*, with patches of short 'turf' formed by *Laurencia pinnatifida*, while *Enteromorpha* is frequently widespread over the beds of mussels. In Saundersfoot Bay extensive sheets of *Sabellaria alveolata* are also found, increasing still further the competition for space and excluding the barnacles to a still greater extent until the community becomes one of *Mytilus-Littorina-Sabellaria* dominance.

To summarize, the Balanoid zone in south Pembrokeshire may be seen:

- (1) In its fundamental form of Chthamalus subzone + Balanoides subzone.
- (2) Completely invaded by fucoids, to the almost complete exclusion of barnacles.
- (3) Partially invaded by fucoids, to give mixed barnacle-fucoid communities.
- (4) Invaded, at its lower levels only, by *Balanus perforatus* and *Fucus serratus*.
- (5) Passing into a cryptofaunal community in the lower part of the Balanoides subzone.
- (6) Invaded by *Mytilus edulis* and *Littorina littorea* to give a *Balanus-Mytilus-Littorina* community; or by *Sabellaria alveolata* in addition to the two molluscs, to give a *Mytilus-Littorina-Sabellaria* community in mid-beach.

C. *The Laminarian zone*

Along most of the coast, from Lydstep Head to Telpyn Point (i.e. excluding the very exposed stretch between Lydstep Head and Manorbier Bay), wherever rocks extend down to low water the Laminarian zone is well developed, with a rich and varied population of plants and animals. Although laminarian weeds may occur as isolated plants on shady north and north-east faces almost up to M.L.W.N., the zone proper does not commence above approximately M.L.W.S + 1 ft. The most obvious difference between the association

and the *Fucus serratus* subzone which frequently occurs above it is the change in weed dominance. Thus *Fucus* tends to die out, while *Laminaria digitata* becomes common, and *Laurencia pinnatifida* tends to be replaced by *Rhodymenia palmata* Grev. Other weeds such as *Lomentaria*, *Chondrus*, *Ulva*, etc., grow as well in the laminarian association as they do in the *Fucus serratus* subzone. In slightly deeper water *Laminaria digitata* is joined by *L. cloustoni* Edmonst., while *L. saccharina* Lamour is more confined to quiet gulley and rock pools. As in Cardigan Bay *Himanthalia lorea* Lyngb. is totally absent, and as Fischer-Piette (1936) remarks, this species does not favour highly sedimented areas.

Where the Laminarian zone is at its best the cover of larger weeds is good, there is a thick undergrowth of smaller weeds, and the animal population is varied. It is possible to distinguish between three separate faunal components: (1) Certain species such as *Sabellaria alveolata*, *Mytilus edulis*, *Nucella lapillus*, *Gibbula umbilicalis*, *G. cineraria*, *Carcinus maenas* (Pennant), *Cancer pagurus* L., *Porcellana longicornis* (L.), *Pomatoceros triqueter* (L.), etc., which are characteristic of the *Fucus serratus* subzone, are equally characteristic of the laminarian community. Other species such as *Balanus balanoides* and *B. perforatus*, *Littorina littorea*, *L. littoralis*, occurring in numbers in the *Fucus serratus* belt, have died out. Of the limpets, *Patella depressa* has completely disappeared, *P. vulgata* is markedly reduced in numbers, while *P. athletica* becomes increasingly common.

(2) A number of species which occur higher up the shore only in shaded and sheltered caves and under overhangs (i.e. in the cryptofaunal community) become, in the Laminarian zone, much less restricted to shady conditions, and emerge more and more into the open as one proceeds lower and lower into the laminarian belt. These include ascidians such as *Botryllus*, *Botrylloides*, *Morchellium* and *Amaroucium* (see p. 133), sponges (see p. 132) and some of the anemones, especially *Tealia felina* and *Metridium senile*. *Alcyonium digitatum* is not only more frequent in its occurrence but the colonies are larger at such low-tide levels. Indeed, the majority of species characteristic of the cryptofaunal association are equally as characteristic of the Laminarian zone of sheltered localities; presumably they succeed in penetrating upwards into the lower Balanoid zone only in conditions of perpetual shade and shelter from surf. The cryptofaunal community may best be interpreted as an upward extension of the Laminarian zone occasioned by local mitigation of the adverse effects of direct illumination, except that the laminarians themselves and other weeds are not included, possibly due to the fact that they require a greater light intensity for photosynthesis than is experienced in such situations.

(3) In this third category are included species entirely restricted to the Laminarian zone, such as *Ascidia virginea* O. F. Müller, *Acmaea virginea* (Müller), *Patina pellucida* (L.), and a few nudibranchs such as *Polycera quadrilineata* (O. F. Müller) and *Facelina longicornis* (Montagu). None of these was taken above the upper limit of the laminarian belt in any locality during the present survey.

The above description applies to the Laminarian zone of sheltered coasts. From Lydstep to Manorbier Headland and in Manorbier Bay the association is of an entirely different type. Here, under conditions of powerful surf action, not only is the weed cover very much reduced but many species of plants and animals typical of sheltered localities are absent. On the vertical seaward faces of reefs and stacks off Manorbier and Lydstep Headlands the Balanoid zone usually passes into one dominated by encrusting calcareous algae and corallines. Lithothamnium extend as pink sheets over what is almost bare rock, with straggling growths of *Corallina squamata* in the cracks. Larger weeds, even *Laminaria*

digitata itself, are thinly distributed, and there is no thick matted undergrowth of smaller weeds. Only the hardier animal species such as limpets and chitons are able to survive, and there is a noticeable absence of the more delicate sponges, hydroids, bryozoans, anemones and ascidians. This is essentially the type of Laminarian zone found in Cardigan Bay, and it is clearly related to the strong and severe pounding by surf which is experienced both in the latter region and along the Manorbier-Lydstep stretch in south Pembrokeshire.

V. DISCUSSION

In comparison with the coast of Cardiganshire, rocky beaches in south Pembrokeshire possess a very rich and varied fauna. The chief differences are to be found in the Balanoid and Laminarian zones of the two regions. A brief comparison of the *Littorina* zones has already been made (see p. 126).

Of the five main types of Balanoid zones which occur in south Pembrokeshire some are also found in Cardigan Bay. The basic form (type 1, p. 127) is met with in several places; type 2 (p. 129), with a heavy cover of fucoid algae excluding the barnacles, is occasional in a few localities near Aberystwyth; and the various forms of mixed barnacle and fucoid communities occur commonly all along the coast. *Balanus perforatus* does not extend up to mid-Wales, therefore the *B. perforatus* subzone is never observed. It is unusual, too, to find a pure barnacle community passing into a belt of *Fucus serratus* at low water. This is largely due to differences in rock configuration on the two coasts. In Pembrokeshire this particular association is developed in response to the local shelter which is afforded by masses of broken rock at the foot of a steep or vertical cliff. This type of beach is not met with in Cardigan Bay. Here the beach is usually fairly wide, with a gentle slope, and since the headlands do not extend very far in a seaward direction, if any shelter at all is experienced it is at the top of the shore, and not at low levels. Consequently, it is more common to find the upper beach colonized by weed (*Pelvetia*, *Fucus spiralis*, *F. vesiculosus*, etc.) passing into an area dominated by barnacles lower down, than it is to find a top-shore balanoid belt giving way to a belt of fucoids (*F. serratus* subzone) below M.T.L. Although *Mytilus edulis* is, for some reason, not particularly common or widespread in mid-Wales, at some places (e.g. near Borth) a mid-beach community with *Balanus balanoides* and mussels co-dominant is to be seen. Areas where *Sabellaria alveolata* and *Littorina littorea* compete with *Balanus* for dominance are even more frequent.

The chief difference between the mid-beach communities on the two coasts is the complete absence of a rich cryptofaunal community in Cardigan Bay. Again it is largely a question of rock formation. I have stressed previously that this particular type of association depends for its existence on the simultaneous mitigation of two adverse factors, those of surf and direct illumination. When this occurs, as it does on north-facing slopes and overhangs and in the shelter of caves on the south Pembrokeshire coast, certain species usually characteristic of the Laminarian zone or of shallow water are enabled to extend up into the lower Balanoid zone. Shelter from direct sunlight involves simultaneous shelter from the heating and desiccatory effects of the sun, and the surface humidity of shady overhangs and caves is undoubtedly much higher than that of open rocks facing the sun. Moreover, it is probable that the thick matted growth of weeds, hydroids, sponges, etc., on these overhangs does much to maintain a damp and humid atmosphere by the retention of water. But shelter from sunlight alone is not sufficient. Thus, along the coast from Old Castle Head to Manorbier, although overhangs, caves, fissures, north-facing slopes and

other shady situations are not lacking, no well-developed cryptofaunal communities can be observed anywhere along this stretch, except on the north-west side of Manorbier Headland (see Fig. 1), where some local shelter from wave action is experienced. In Manorbier Bay itself, north-facing overhangs are infrequent, surf action is still powerful, and again the association is lacking. Both shade and shelter from surf are necessary.

This accounts for the absence of such communities in Cardigan Bay. To begin with, the 'over-all' exposure to wave action is too great, as it is on the Old Castle Head-Manorbier stretch of south Pembrokeshire. Secondly, it is rare to find simultaneous shelter from sunlight and surf. The coast of mid-Wales faces almost due west, and while the prevailing winds are, admittedly, from the south-west, wind and gales from the north and north-west are by no means infrequent (Evans, 1947*a*, fig. 3). Yet here, as in south Pembrokeshire, the shadiest faces are on the north side of reefs, etc. On the latter coast the beach is protected from northerly winds and gales, but in Cardigan Bay no such shelter is experienced, therefore localities experiencing maximum shade and maximum shelter simultaneously are not generally met with. Again, the strike of the shore strata (generally parallel to the sea) in Cardigan Bay, and the direction of dip (generally toward the land) are not encouraging to the existence of any association which includes delicate species such as the sponges, coelenterates, bryozoans or ascidians. If the dip were steep and seaward, one might expect, as Walton (1915*b*) suggests, a fairly rich fauna on the shady and sheltered landward overhangs, but such conditions do not occur. Even in the gulleys and inlets between reefs on the lower shore, where shade and shelter might occasionally coincide, the effects of constantly moving shingle have still to be overcome, for most of these gulleys contain loose drift material.

It is, perhaps, worth noting that the waters of Cardigan Bay are, for the greater part of the year, characteristically turbid, and this has been suggested as a contributory cause of the absence of various common intertidal animals. Without greater knowledge of the habits and requirements of such animals it is difficult to assess the precise significance of this factor, but from personal observation I am inclined to believe that the effect, if any, can only be very slight. There are localities both in north and south Wales (and elsewhere) where, although the silty coating of the shore rocks testifies to the generally high degree of sedimentation of the water, the richness and variety of the littoral associations seem to be in no way impaired.

I would suggest then that the above are adequate reasons for the absence of the crypto-faunal association in Cardigan Bay.

The Laminarian zone in south Pembrokeshire, as I have remarked above, is quite different in the region Lydstep Head to Manorbier Bay and on the stretch of coast farther east. In Cardigan Bay this zone is essentially similar to the form it takes under exposed conditions in south Pembrokeshire (see p. 134), where it is populated by the hardiest species only, and where weed cover is thin and sparse. Again this appears to be related to the lack of adequate shelter from surf. Not only is the factor of 'over-all' exposure to wave action discouraging, but also the short headlands which are typical of the coast of mid-Wales do not extend seaward far enough to create areas of local shelter on the lower part of the beach in the small rocky bays. The movement of loose shingle in low-tide gulleys and inlets must, again, be counted as an adverse factor.

At such low-tide levels, shelter from direct illumination and its desiccatory effect is less important than it is higher up in the Balanoid zone, for such levels are comparatively

rarely exposed to the air. Thus shelter from surf is the chief prerequisite for the occurrence of a rich laminarian community.

On all British coasts the Laminarian zone is usually the richest from the point of view of the variety of species it contains, and in south Pembrokeshire the cryptofaunal community may be regarded as an upward extension of this zone. In Cardigan Bay, not only is the Laminarian zone barren of the more delicate elements of the fauna, but no counterpart to the cryptofaunal population exists. Thus the lower shore, where one might expect to find the greatest variety of littoral species, is disappointingly bare, and this is undoubtedly the chief reason for the poverty of the littoral fauna on the coast of west Wales. The peculiar local conditions which lead to this state of affairs may be summarized briefly:

(1) The very high degree of exposure to wind and surf, which is paralleled with similar results on the Lydstep Head-Manorbier Bay stretch of the south Pembrokeshire coast.

(2) The westward orientation of the coast offers no shelter from gales and winds from the north and north-west.

(3) The absence of overhangs, fissures, caves, etc., where shelter from surf and sunlight may be experienced simultaneously.

(4) The lack of shelter on the lower beach, which is due to the smooth outline of the coast and the absence of projecting headlands.

(5) The scouring and abrasive action of loose drift material in gulleys, etc., where some measure of shelter is, admittedly, experienced.

VI. SUMMARY

1. A survey of approximately 15 miles of the south Pembrokeshire coast has been made for comparison with the shores of Cardigan Bay, and in order to discover what factors may be responsible for the poverty of the littoral fauna in the latter region.

2. The geography and geology of the area included in the survey are dealt with, and the factors of climate, tidal range, and exposure to surf are compared for the two coasts.

3. The Littorina, Balanoid, and Laminarian zones of south Pembrokeshire are described. The Balanoid zone occurs in five different forms, some of which are also met with in Cardigan Bay; others, notably the development of a 'cryptofaunal community', have no counterpart on the Cardiganshire coast. The Laminarian zone is found to be entirely different on the exposed shores between Manorbier and Lydstep than it is under more sheltered conditions farther east.

4. The cryptofaunal community is described in detail; it is shown to possess a rich variety of species, the majority of which are rare or unrecorded in Cardigan Bay. The same is true of the Laminarian zone; on the coast of mid-Wales it takes essentially the same form as it does on exposed stretches on the coast of south Pembrokeshire.

5. The poverty of the littoral fauna in Cardigan Bay is explained by the absence of the cryptofaunal community and of a well-developed Laminarian zone.

6. The reasons for the poor development of such associations on the Cardiganshire coast are discussed, and it is concluded that they are related to the following factors:

(a) The high degree of exposure to surf which is experienced all along the coast.

(b) The westward orientation of the coast results in lack of shelter from north and north-west gales and winds.

(c) Combined with the westward orientation of the shores there is a general lack of caves or overhangs where maximum shelter from surf and maximum shade may be experienced

simultaneously, for shady north faces are not protected from surf as they are on the south-facing shores of Pembrokeshire. Thus the conditions necessary for the development of cryptofaunal associations are not experienced.

(d) The smooth outline of the coast and the absence of long sheltering headlands do not favour the existence of a rich population of more delicate animals in the Laminarian zone.

(e) The scouring and abrasive action of loose shingle tends to denude the sides of gulleys and channels where shade and shelter might be sufficient to allow the development of a rich fauna.

(f) The generally high degree of sedimentation and the turbidity of the water may exert some adverse effect on the intertidal fauna.

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THE SPREADING OF THE BRITISH FLORA CONSIDERED IN RELATION TO CONDITIONS OF THE LATE-GLACIAL PERIOD

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Advance in solution of the manifold problems of interpreting the distribution of the components of the British flora is apparently suspended until we may resolve the old dilemma of the extent to which the species now in these islands survived the last Ice Age here (possibly in areas they now occupy), and, conversely, of the extent to which they have had to re-immigrate. Over this issue powerful arguments have been raised for and against per-glacial survival, but as may be judged from the report of the Royal Society discussion upon this topic in 1935, agreement has never been within sight.

This paper is written in the belief that the evidence now being brought to light by studies of conditions in the Late-Glacial period, go a considerable way to resolve the problem, and, indeed, to show how the arguments of both schools may be reconciled. In large part the evidence consists of identifications of fruits, seeds and pollen grains from sites which, on grounds of stratigraphy, flora, and fauna are known with fair certainty to have formed in the Late-Glacial period or at the opening of the Post-Glacial period. These identifications, in part, are already published, and in part have been made in the sub-department of Quaternary Research in Cambridge, and will be published fully in due course.

I am much obliged to my colleagues and students for permission to mention in this general way some of the identifications they have made.

A very brief summary in *Science Progress* (Godwin, 1947) draws attention to the substantial recent advance in our knowledge of Late-Glacial conditions in north-west Europe. The period is defined as that between the commencement of retreat of the ice from Denmark and northern Germany up to the beginning of retreat from the great central Swedish end-moraines. It has been shown that after this latter date, approximately 8500 B.C., woodland cover existed over southern Scandinavia, but before this the landscape was one of tree-less tundra, or of tundra broken by small copses of tree-birches, the 'Park-tundra' of Iversen. A temporary amelioration of climate, followed by a recession during the Late-Glacial period, has been widely recognized and is described as the Allerød oscillation. During this warm phase more or less closed birchwoods were found in southern Denmark and pinewoods grew in Holstein.

In the cold periods before and after the Allerød warm stage 'cryoturbatic' phenomena are widely recognized; it is evident that solifluction was prevalent and that the open soil surface was much exposed to displacement by frost, water and wind, whilst big spreads of gravels, sands and loess afforded sites for temporary establishment of plants. Macroscopic remains from these periods show abundant *Dryas octopetala*, *Betula nana*, *Salix herbacea*, *Armeria vulgaris*, *Empetrum nigrum* and plants of similar character, but it is from pollen analyses, now abundant, that one can reconstruct the general character of the vegetation. Pollen of herbaceous plants greatly outweighs that of trees (birch and pine), and a large part of it consists of grass and sedge pollen. In addition, the pollen grains of many herbaceous plants

occur in unexpectedly high frequencies, and as we become more skilled in their recognition, it is apparent that they are present also in much variety. Genera represented abundantly and widely are *Artemisia*, *Rumex*, *Thalictrum* and *Helianthemum*. The vast stretches of this 'park tundra' afford a clear explanation of the prevalence at this time of the fauna of giant herbivorous mammals, horse, reindeer, bison, elk and giant Irish deer. Their remains occur very abundantly in deposits of this period, but become infrequent in the following forest period when not only was pasture greatly restricted, but predators were favoured by woodland conditions, whilst it is possible also that maturation of podsol profiles from raw soils had its effects upon animal nutrition. Beside watercourses and in drainage basins there was an abundant aquatic and marsh vegetation, whilst in the Allerød warm phase the mineral soils appear to have been stabilized by continuous vegetation cover, and pure organic nekron-muds (*gyttja*) formed in the lakes. Similar conditions followed the Allerød cold phase at the opening of the final post-glacial climatic amelioration.

It has become clear also in recent years that we must replace our former conception of glacial retreat as a step-by-step withdrawal of a continuous ice-front exposing a widening strip of bare soil, by a picture (at any rate for a large part of the Late-Glacial period) of sheets of dead ice decaying *in situ*, often covered with gravel and sandy debris and even vegetation-clad before their final disappearance.

These various phenomena are of course at once a record of the precise nature of vegetation at a former period, and a challenge to revise our theories of vegetational migration and establishment in the light of new knowledge of environmental conditions in the pre-forestal stage of development after the Ice Age.

There can be no question that these findings of Scandinavian research apply to the British Isles also. The Allerød oscillation has been recognized in various stratigraphic circumstances in England; Mitchell has reported it from southern Scotland, whilst in Ireland, Jessen, Mitchell and Farrington have recorded many instances of it. Whilst we await eagerly the publication of Jessen's extensive Irish investigations, he has already publicly disclosed sufficient of his findings to convey the general character of the Late-Glacial in Ireland, and something of his views upon the phytogeographic problems of that country (British Ecological Society Report, 1947).

The pollen zones I, II and III employed by Jessen in Denmark respectively for the stages of lower Dryas clays, lake-muds, and upper Dryas clays of the Allerød oscillation have been employed by him for Ireland, and are in use for England also (Pennington, 1947).

With this by way of reference to the general background of knowledge of Late-Glacial conditions, let us turn to closer consideration of the English evidence.

At Nazeing, in the Lea Valley just north of London, we have investigated Late-Glacial deposits of open-water muds which rest upon gravels containing the well-known rafts of 'Arctic bed' investigated by Clement Reid, Mrs Reid and Miss Chandler, and which pass conformably upwards into peats exhibiting the pollen zonation of the early Post-Glacial period and then of the Post-Glacial warm period. The lowest of these mud layers are clearly either Late-Glacial or Early Post-Glacial in date. From them Miss J. Allison and I have secured a remarkably long list of plant identifications (over 78 species plus 22 genera). They are mostly based upon fruits, seeds or leaves for which specific identity can be established, and they are evidence of plant growth not far from the locality of discovery. In this respect they differ from the pollen identifications which often cannot be extended

beyond the genus, and which, on account of the easy flight of pollen, may represent plants growing at a considerable distance, especially where single grains alone have been encountered. The plants identified clearly belong to three main categories: (1) 'arctic-alpine' forms,* such as *Dryas octopetala*, *Betula nana*, *Arenaria ciliata*, and *Thalictrum alpinum*; (2) aquatic and marsh plants, such as *Potamogetons*, *Myriophyllums*, *Filipendula ulmaria*; and (3) species now regarded as ruderals, or as weeds.

Both categories of land plants consist of species intolerant of competition, and this accords with the absence of forest cover at this time. So far also as the ruderals and weeds require constant exposure of fresh soil surfaces, these were certainly available in general in Late-Glacial times, as it is clear that they were at Nazeing.

The 'ruderals and weeds' include many species which it is surprising to record so early in the history of the British flora, for many of them at the present day appear so restricted to special crop and roadside habitats that we have assumed they were introduced by Neolithic or later invasions of races practising plant and animal husbandry.

Late-Glacial finds at Nazeing have thus assured native status to such plants as *Sonchus asper*, *Polygonum aviculare*, *Galeopsis tetrahit*, *Chenopodium album*, *Potentilla anserina*, *Ranunculus acris*, *R. repens*, *Taraxacum officinale*, *Linaria vulgaris*. The very unmistakable seeds of *Linaria vulgaris* have also been recovered from Late-Glacial beds near Huntingdon, and pollen of *Artemisia*, *Chenopodium*, *Matricaria* (type) and *Rumex* occurs in the Late-Glacial deposits in Cornwall, together with fruits of *Carduus nutans** or *C. crispus*.

If we accept the 'arctic-bed' records of C. and E. M. Reid and Miss Chandler as also belonging to this period, the list of ruderals and weeds will be longer. If these as well as our own lists fruits of the genus *Carduus* occur, and although there may be some doubt about reference to species, many are, of course, weeds or ruderals. In the characteristic herbaceous pollen assemblage of the Late-Glacial period, the genus *Artemisia* is always very strongly represented, and it is interesting to find that it becomes again of importance when Neolithic forest clearance has taken place. Composite pollen of various types is present, and that of the *Matricaria* type can hardly be derived from other than plants of the ruderal and weed category.† Much clearly could be pollen from species also recorded from fruit identifications.

Iversen recently reported the identification of pollen of *Centaurea cyanus* (cornflower) from three different Danish Late-Glacial sites, and Mr P. A. Tallantire has recently recovered a grain of it also from a Late-Glacial deposit in the East Anglian Breckland. It cannot be confused with grains of other species of *Centaurea*.

It seems very probable that as our identifications of Late-Glacial fossils extends, more and more of our ruderal and weed species will be recognized as long native to the British flora, and this may prompt a reconsideration of their status in habitats such as marine and mountain cliff and scree-slopes, sand-dunes, shingle-ridges, river-banks and mountain habitats above the tree-line. It seems more than likely that in these situations these species may have their 'natural' occurrences, and they are not to be explained merely as recent colonization from agricultural ground, or as response to recent introduction.

Among the ruderal and weed species, as also among the marsh plants, it is to be remarked

* The term 'arctic-alpine' is employed for this category of plants because this is the usual and convenient designation, although it is an inadequate expression of their distributional range.

† *Matricaria maritima*, although not a ruderal or weed, is characteristic of open habitats, i.e. shingle banks, maritime cliffs, and to a less extent sand-dunes, and it must be closely related to *M. inodora*.

that there are many of considerable size; thus, besides large sedges (of which *C. rostrata* is very commonly the most abundant), we have *Filipendula ulmaria*, *Ranunculus lingua*, the species of *Carduus*, *Sonchus* and *Ranunculus* already mentioned, and species of *Centaurea*, *Succisa*, *Epilobium*, *Galeopsis*, *Valeriana*, *Campanula*, etc. Such plants suggest a favourable growing season with abundant water, and incidentally indicate that the pasturage of the big mammals was by no means meagre.

The concurrence of the three floristic elements found at Nazeing is one familiar to-day in northern Scandinavia in sites where a particular conjunction of climate, soil and topography occurs. On this soil over basic (perhaps calcareous) rocks the 'arctic-alpine' species are found, on the disturbed soils of the slopes there are 'ruderals and weeds', in the wet valley bottoms are luxuriant fen and marsh communities, and sheltered localities harbour patches of birch woodland. It will be noted that the raw soils of the Late-Glacial will in general be rich in bases.

The arguments upon which per-glacial survival *in situ* are based depend rather largely upon the local or restricted distribution area of certain rare species, whose occurrence in regions such as Teesdale is held explicable only on the ground that they survived in place whilst such areas were unglaciated refuges.

Examination of Late-Glacial deposits has now resulted in the identification of several species widely beyond their present-day area in Britain. Perhaps the most striking instance is the recognition of pollen of *Polemonium*, which was first recognized by Miss R. Andrew at Nazeing, where in some layers it is quite abundant. It does not seem possible to distinguish between the pollen of *P. caeruleum* and *P. humile*, but the reference to this genus is unmistakable. This pollen has since been found by Miss Andrew in Late-Glacial or Early Post-Glacial muds from Cornwall; from Hockham Mere, Norfolk; and from Old Decoy, close to the conjunction of the Norfolk, Suffolk and Cambridgeshire county boundaries. *P. caeruleum* has now a very restricted range in the limestone country of the north of England, and has sometimes been regarded as an escape from cultivation. It is clear that on the contrary it was native long since, and that once widespread it has suffered much restriction of area. Should the pollen indeed be that of *P. humile* the restriction of area is of course greater, for *P. humile* is now found only in very northern localities outside Britain.

A discovery of similar character is that of fruits of *Thalictrum alpinum* at Nazeing, and in Cornwall. Furthermore, pollen of *Thalictrum* (though not necessarily *T. alpinum*) is almost always present in Late-Glacial deposits. Similarly fruits, cone-scales or leaves of *Betula nana* occur at the base of Breckland meres (P. A. Tallantire), in Cornwall, and abundantly in the Lea Valley. Likewise, *Salix herbacea* occurs in Cornwall.

From the Lea Valley Miss J. Allison has identified an achene of *Potentilla fruticosa* and a nutlet of *Teucrium scordium*, and leaf fragments (and possibly achenes) of *Dryas octopetala*. From the Late-Glacial bottom of a Norfolk mere P. A. Tallantire has recovered a seed of the very rare or extinct *Holostium umbellatum*.

These instances do not exhaust the list of identifications; the number grows continually and clearly will continue to do so. Already, however, one result is fully apparent. Many species now of restricted range were widespread in the pre-forestal conditions of Late-Glacial times; their present distribution must be considered as having been contracted and broken up in the Post-Glacial period. This process seems most reasonably interpreted in terms of two factors: first, and most important, the effect of dense forest establishment and persistence through the period of the post-glacial climatic optimum, and secondly, the

development of peat mires upon flat and gently sloping mountains at altitudes above the forest limit. We have little knowledge that such peat mires (chiefly of the nature of blanket-bog) occupied these areas in Boreal or Pre-Boreal times, but it has become clear that they were developing in many areas in the early part of the Atlantic period (i.e. the early part of Zone VII in the British zonation). As a third factor might be added the disappearance of soils of suitable status, since many species regarded as having relict distribution appear to be calcicolous, or at least to demand soils of high base content.

Such considerations at once alter our interpretation of such phenomena as the Teesdale 'refugium'. This area, whilst retaining its character as a refuge for a remarkable assemblage of arctic-alpine species, is interpreted as preserving them not through the rigours of the last glacial period, but through the post-glacial forest period until the recent period of disforestation and increased pasturage. Correspondingly, the period of widespread occurrence (before the isolation of such groups of species) is now envisaged not as an interglacial or pre-glacial one, but as the Late-Glacial and Early Post-Glacial. I do not now propose to consider in what ways Teesdale might be suited to serve as a refugium through a forest period of species demanding open conditions, but it does have evident qualifications for this.

The interpretation of glacial refugia has always been bound up with questions of the rates of spread of species under natural conditions. Those favouring per-glacial survival *in situ* have held to the view that natural spread is extremely slow, and their opponents have held it inadmissible to explain phytogeographic range phenomena by any assumption of inadequacy of dispersal mechanism. The arguments based upon these Late-Glacial identifications force us to recognize a situation in some respects combining these conflicting views. In the Late-Glacial and early Post-Glacial periods themselves the rates of migration of higher plants must have been exceptionally fast into the very abundant habitats made available by melting ice and snow and resorting of glacial and peri-glacial superficial deposits. Such rates of spread must have been comparable with those of modern instances of spread into land laid bare by man's activities. By contrast, in the ensuing period of dense afforestation, these species of open habitats were heavily restricted and isolated, and their rates of spread across forest areas must have been very much diminished. Only in recent times of anthropogenous disforestation has the spread of the open habitat species become once more rapid and easy. Naturally within the forest period the species characteristic of deciduous woodlands found *their* opportunity for rapid spread, an opportunity absent alike in the preceding treeless period and in the present period of forest regression and discontinuous woodland (see, for example, the influence of woodland disintegration upon distribution of the oxlip and primrose as described by Valentine, 1948).

This concept of alternation of phases of rapid and general dispersal with phases of fixity, seems to add much to our resources in interpretation of contemporary distribution phenomena, whilst avoiding the impasse of substantial but contradictory hypotheses which hold the field at present.

The concept of succeeding phases of very different dispersal rates has great interest in relation to the operation of substantial natural barriers to plant migration, such as the North Sea and the Irish Sea, in relation respectively to the colonization of Great Britain and of Ireland.

A fall of 300 ft. in ocean level at the present day would expose two narrow land bridges between north Wales and the Irish coast, as well as a broader land-belt between north-

western Ireland and south-west Scotland. A fall of 400 ft., however, would mean that apart from a narrow lake off north-east Ireland, the area of the Irish Sea and English Channel would be entirely dry, and 400 ft. is, indeed, a modern conservative estimate (Farrington, 1945) of the eustatic fall in ocean level due to the locking up of water in the ice-sheets of the glacial period. It must be recognized that the same climatic amelioration which rendered the land available for recolonization by plants and animals also restored the sea barriers which presently impeded migration, and that we do not know the precise relationship of these two processes. It has become clear, however, through the results of pollen analysis of peat now lying in at least 174 ft. of water that in Late-Glacial and early Post-Glacial times the bed of the North Sea was still dry land. The conditions of open ground thus extended across from north-west Europe in the period of rapid plant distribution; by the time, however, that the North Sea had reached its present extent, forest growth was widespread over the British Isles, and dispersal of all save woodland species had become very restricted.

Thus freedom of movement of plant species in the Late-Glacial and early Post-Glacial period was enhanced by the fact that the North Sea was then dry land, whilst difficulty of movement in the ensuing Post-Glacial period was accentuated by the fact that the North Sea and Irish Sea had then reached their present size.

In view of these circumstances it is not surprising that Praeger (1934) should find two categories of British plants particularly under-represented in Ireland, namely, the woodland plants and plants of southern distribution in England, that is to say, species unable to spread early because of temperature limitations. Both categories must have been post-glacial as opposed to late-glacial immigrants. Of the woodland plants he writes: 'Thus, for instance, the poverty of the woodland flora of Ireland is conspicuous as compared with England or Scotland—no *Helleborus*, *Linnaea*, *Trientalis*, *Daphne*, *Corallorhiza*, *Goodyera*, *Cephalanthera grandiflora*, *Maianthemum*, *Ruscus*, *Convallaria*, *Paris*.' We may dissent from his view that this poverty is essentially due to destruction of forest by the hand of man; we have, however, attempted no analysis of distribution data of Irish species in relation to the new viewpoint.

We have mentioned earlier that there appears to be close agreement in character between the list of identifications we have obtained from undoubted Late-Glacial layers at Nazeing and the aggregate list compiled by Mrs E. M. Reid (1949) for the various exposures of the rafts of 'Arctic bed' material which have been found in the Lea Valley. Although the latter are older they may nevertheless perhaps still be regarded (as they have hitherto been) as Late-Glacial. If so, it would appear that some species which lived in Britain in Late-Glacial times, no longer do so. These include *Ranunculus hyperboreus*, *Potentilla nivea* and *Silene caelata* (the latter not known living). That the Post-Glacial forest period should be a period not only of restriction of many species but even of extinction of some is, indeed, a natural extension of the thesis we are outlining. It is possible that some species have been lost because they had a definite 'cold requirement' (a demand not easy to visualise in physiological terms), or more probably because they were intolerant of competition. It is interesting to note that research in Ireland has also disclosed the extinction of species within the Late-Glacial period. *Naias marina* once found in the Late-Glacial layer at Lough Gur is no longer native (Praeger, 1934), and Mitchell (1942) has reported the discovery of *Betula nana* which also is not now found living in the country.

One ought, however, to acknowledge that the evidence from the aggregate lists for the 'Arctic bed' material of the Lea Valley is complicated by the possible presence of derived material, although there is no special reason to regard as secondary the three species mentioned.

Let us finally turn to consider how the views we have developed relate to the disputed issue of per-glacial survival. It appears that by the new approach we do not indeed solve the problem of per-glacial survival of the British flora, but indicate the irrelevance of this issue for a considerable part of the plant population. By establishing the existence over a wide range of territory of species to-day restricted in area, we define our problem as essentially one of post-glacial movements and adjustments, rather than of per-glacial survival. It does, indeed, matter scarcely at all whether a given species actually survived the latest glaciation in the south of England, if, as we suppose, it might with great facility have entered from the continent in the Late-Glacial or early Post-Glacial period.

Now that we infer from our reconstruction of conditions at the time how easily species might have spread, and have learned from fossil records how widespread certain plants were, it must be agreed that migration from the continent was easy in this period. It therefore has become of much less importance to know whether a given plant was present in Britain throughout the last Ice Age; the crucial point is rather the effect upon these widespread plants of the following Post-Glacial period of dense forest growth.

In stating the matter thus I am far from saying that it is of no importance to know what was happening to the flora during the Glacial periods; still less would one deny the possibility or likelihood of per-glacial survival for certain species. Indeed, one may well inquire whether there is any possibility that conditions throughout the latest glaciation might not, in the peri-glacial region of the south of Britain, have resembled those now described for the Late-Glacial period; this is, of course, a matter for research rather than speculation.

Nor, naturally, do I attempt to deny that the limits of distribution of many species are clearly determined by the operation of climatic, edaphic or topographic factors operating in manners more or less familiar to ecologists. We are concerned rather with *problems* of distribution not altogether soluble by reference to such factors, and to the unknown history of the flora. What arises now is a reconsideration of distribution processes and distribution periods as they have affected phytogeography. This reconsideration is forced upon us by a growing body of evidence from subfossil plant material, of distribution areas at particular times in the past. Whilst we look to such studies to extend our proofs of former movements of the flora of Britain, it may be hoped that the results already evident will be found to help analysis of the phenomena of geographical distribution, and perhaps to reveal new fields of inquiry.

My warm thanks are due to Prof. A. R. Clapham and Dr A. S. Watt for beneficial criticism of this note.

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RINGINGLOW BOG, NEAR SHEFFIELD

PART II. THE PRESENT SURFACE

By VERONA M. CONWAY, *Department of Botany, Sheffield University**(With ten Figures in the Text)*

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1. DESCRIPTION OF THE VEGETATION

In the first part of this paper, some account was given of the structure and history of Ringinglow bog (Conway, 1947). The data indicated that the original mineral surface, on which the peat lies, was a gradual slope with one well-marked trough or valley, and another, less distinct, running parallel to the main one and north of it. A study of the bog surface suggests strongly that this drainage pattern is still determining the distribution of the main types of plant community. These are indicated broadly in Fig. 1, except that *Eriophorum vaginatum* is not shown because it is present almost everywhere on the bog. It is not of course everywhere equally prominent; where *Calluna vulgaris* is dominant, the cotton-grass may be present, on any one metre-quadrat, only as a single sad-looking tuft. Nevertheless, its status over the bog as a whole may be judged by the fact that out of 370 quadrats listed in various parts of the bog other than the Juncetum, only five lacked *Eriophorum vaginatum*.

The vegetation map shown in Fig. 1 is essentially a sketch-map, though it is based on the survey from which the contours were constructed, and confirmed by transects along the lines *AB*, *CD* and *EF*, which will be described presently. The survey was not sufficiently detailed for accurate mapping of the drainage channels, and since the publication of Part I of this paper the sketching of the drainage channels has been revised; this accounts for one or two minor discrepancies between the present map and those appearing in the earlier publication.

It will be obvious that the vegetation map is highly simplified. This was inevitable on account of the size of the bog, but it may not be a disadvantage, since it gives expression to the features that are ecologically most important. There are, first of all, two areas in which *Eriophorum angustifolium* is consistently present, and these may be considered as the two chief flush areas of the bog. The word flush is here used in a broad sense to denote

a region lying above the head of a visible drainage channel, a region which forms the gathering ground for the water which will run off down the channel. There is no implication that the soil water must necessarily have a higher base status than that found in surrounding areas.

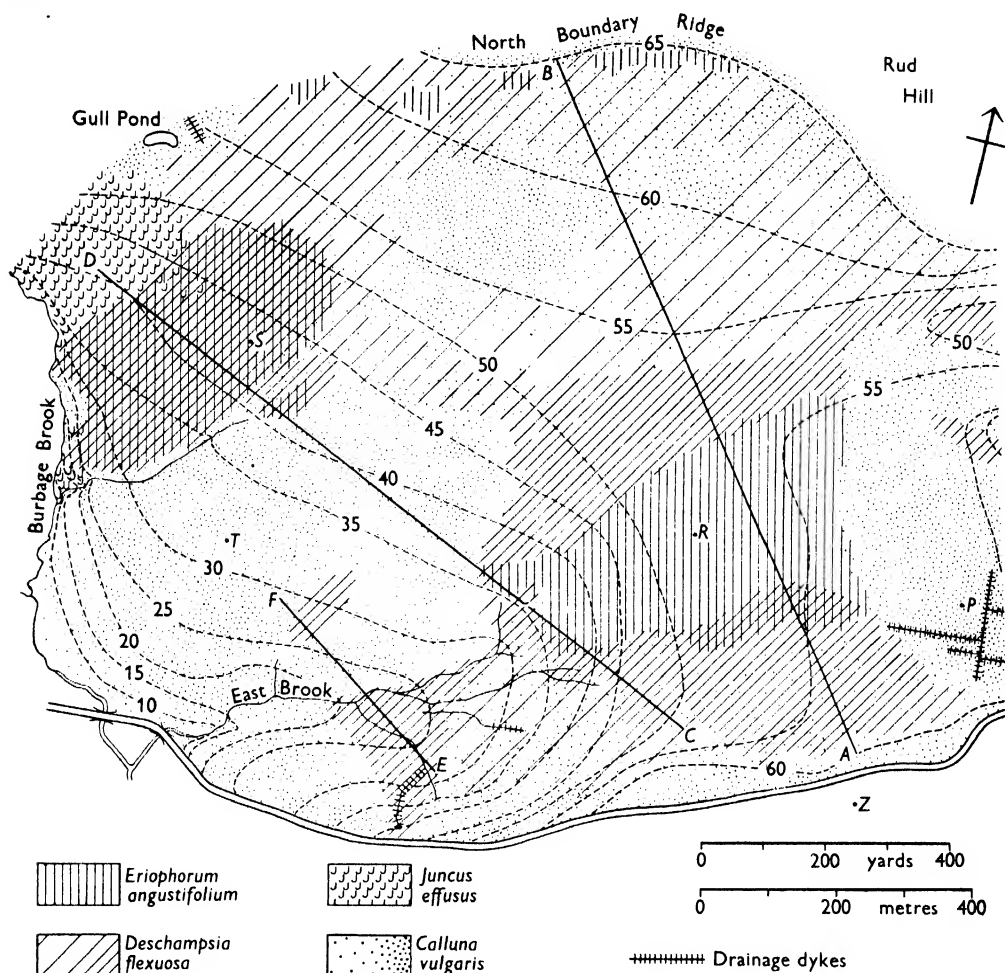


Fig. 1. Sketch-map of the main vegetation types on the bog, *AB*, *CD*, *EF*, transects which gave the data shown in Figs. 2, 3 and 4. *R*, *P* and *Z*, sites of water-level pits and pH sampling, giving the data for Fig. 7. *S* and *T*, sites of water-level pits giving the data for Fig. 5.

We have then, first, the main flush, or central Eriophoretum, lying more or less centrally in the eastern half of the bog and supplying water to East Brook, and, secondly, the north-western flush, which drains into Burbage Brook and its eastern tributary. Between the two is a watershed dominated by *Calluna*, which dominates also the watershed running north from the road to Rud Hill and forming the eastern edge of the area studied. *Calluna* is abundant, too, around the bog margin and in other places where the slope gives adequate drainage.

The frequencies given in Table 1 will indicate the floristic character of the bog vegetation. The poverty in species needs little emphasis, since this feature of the south Pennine peat moors has long been recognized.

(a) *The main flush*

Although Fig. 1 suggests that *Eriophorum angustifolium* is the dominant in the centre of the flush, it is *E. vaginatum* which, in fact, plays this part, although the former species is abundant, showing a frequency of 90% along the relevant part of the line *AB*. The lower figure shown in Table 1 is due to the fact that the quadrats for this estimate lay somewhat towards the margin of the flush area. The central part of the flush is the wettest region of the whole bog, and between 1941 and 1946 it was noticeable that patches of *E. vaginatum* were in a moribund state. Sometimes as much as a square metre would be without live vegetation, and often tussocks with some still live shoots could be lifted by the leaves from the bog surface without any effort. However, the hot dry summer of 1947 had a remarkably stimulating effect, and in 1948 all the *E. vaginatum* appeared healthy, and new green shoots were spreading over the surface of what must previously have been moribund tussocks. *E. angustifolium* also appeared more luxuriant, and had probably colonized many of the wet lifeless hollows which had previously been so noticeable.

Surrounding the central region in which *E. angustifolium* is so abundant, there is a zone in which *Deschampsia flexuosa* is very conspicuous. The tussocks of *Eriophorum vaginatum* tend to be slightly higher here than in the centre, and the *Deschampsia* grows from a creeping mat of rhizomes which lies at a level of 1–3 in. above the bases of the live cotton-grass shoots. The grass roots are found amongst the debris in the top of the cotton-grass tussock, and it is unlikely that they become submerged in water except for a short time on very rare occasions.

This type of vegetation extends southwards, with occasional patches of *Calluna*, right up to the marginal slope which comes down to the bog from the road. To the north, it merges into a wide region of a rather indefinite vegetational type which occupies the north-eastern sector of the bog. Here no one species is dominant over the whole area, and although *Calluna* is everywhere abundant and locally dominant, small wet patches of *Eriophorum angustifolium* are not infrequent, and the whole community gives a mixed and patchy impression. For this no reason is immediately apparent.

The data shown in Fig. 2 bring out some of these points. They are derived from the process of listing the phanerogams on a metre quadrat every ten paces along the line *AB*. *E. angustifolium* and *Deschampsia flexuosa*, if present, were noted as either abundant, frequent, or scanty, showing one or more inflorescences, or none. These subjective estimates were given numerical equivalents, and a record of abundant, with one or more inflorescences, scored the maximum of four for one quadrat. The scores for five consecutive quadrats were added, and the graph shows the scores for these groups of five quadrats. For *Calluna* and *Empetrum nigrum* the quadrats were similarly grouped, but only presence or absence was noted, and the maximum score for a group of quadrats is five.

The left half of Fig. 2 represents that part of the line *AB* which lies across the main flush. It shows very clearly the complementary behaviour of *Eriophorum angustifolium* and *Deschampsia flexuosa*. The right-hand side of the figure shows how, in the northern half of the transect, the maximum density of *Calluna* has a clearly depressant effect on the growth of *Deschampsia flexuosa*. The data show also the widespread, if nowhere abundant, occurrence of *Empetrum nigrum* at this end of the bog.

One last fact, perhaps the one of most interest about the main flush, remains to be stated, or rather to be re-emphasized, since it has been described already in the first part of the

paper. It is the fact that the dominance of *Eriophorum vaginatum* is relatively recent. The present cover consists of tussocks rising from 3 to 6 in. (7–15 cm.) above the general surface of the intervening peat. This surface is the top of a layer of cotton-grass peat

Table 1. *Percentage frequencies of species in metre quadrats*

(1) *Eriophorum vaginatum* dominant with much *E. angustifolium*. (2) *E. vaginatum* dominant with much *Deschampsia flexuosa*. (3) *Eriophorum* spp. with *Deschampsia flexuosa* and *Sphagnum recurvum*. (4) *Juncus effusus* dominant. (5) Patches in the Juncetum in which *J. effusus* was not dominant.

Region of the bog ...	Main flush		South-west Callunetum	North-western flush		
	1	2		3	4	5
No. of quadrats ...	20	20	20	20	20	40
<i>Calluna vulgaris</i>	—	8	100	15	15	2
<i>Empetrum nigrum</i>	10	24	—	—	—	2
<i>Erica tetralix</i>	—	4	5	—	—	—
<i>Oxycoccus quadripetalus</i>	10	24	—	45	5	10
<i>Deschampsia flexuosa</i>	15	100	—	100	95	75
<i>Eriophorum angustifolium</i>	45	52	5	80	5	50
<i>E. vaginatum</i>	100	100	100	100	10	27
<i>Sphagnum recurvum</i>	—	—	—	75	85	80
<i>Campylopus flexuosus</i>	10	8	15	5	—	—
<i>Dicranella heteromalla</i>	—	16	—	—	—	—
<i>Hypnum cupressiforme</i>	—	—	10	—	—	—
<i>H. fluitans</i> agg.	—	—	—	25	—	5
<i>Plagiothecium elegans</i>	—	—	5	—	—	—
<i>Polytrichum commune</i>	—	4*	—	—	20	—
<i>Webera nutans</i>	25	84	55	20	40	15
<i>Calypogeia trichomanis</i>	80	88	70	65	50	22
<i>Cephalozia bicuspidata</i>	75	88	20	85	—	10
<i>Gymnocolea inflata</i>	10	—	—	—	—	—
<i>Lepidozia reptans</i>	—	—	15	—	—	—
<i>Caltha palustris</i>	—	—	—	—	5	2
<i>Cirsium palustre</i>	—	—	—	—	—	2
<i>Galium saxatile</i>	—	—	—	—	50	2
<i>Lotus uliginosus</i>	—	—	—	—	—	2
<i>Menyanthes trifoliata</i>	—	—	—	—	5	5
<i>Potentilla erecta</i>	—	—	—	—	15	15
<i>Rumex acetosa</i>	—	—	—	—	45	15
<i>Viola palustris</i>	—	—	—	—	15	—
<i>Agrostis stolonifera</i>	—	—	—	—	65	72
<i>Anthoxanthum odoratum</i>	—	—	—	—	10	12
<i>Carex curta</i>	—	—	—	—	—	22
<i>C. nigra</i>	—	—	—	—	—	10
<i>C. panicea</i>	—	—	—	—	—	2
<i>C. vesicaria</i>	—	—	—	—	25	17
<i>Holcus mollis</i>	—	—	—	—	—	5
<i>Juncus acutiflorus</i>	—	—	—	—	—	5
<i>J. effusus</i>	—	—	—	—	100	17
<i>Luzula campestris</i>	—	—	—	—	—	2
<i>Molinia caerulea</i>	—	—	—	—	—	2
<i>Nardus stricta</i>	—	—	—	—	—	5
<i>Equisetum fluviatile</i>	—	—	—	—	—	7
<i>Sphagnum cymbifolium</i>	—	—	—	—	5	—
<i>Hypnum stramineum</i>	—	—	—	—	35	10

* *Polytrichum formosum* was subsequently recorded from this part of the bog by another worker, and it is possible that the specimen giving this entry was wrongly recorded as *P. commune*.

which is everywhere present, usually to a depth of 4–5 cm., and nowhere more than 10 cm. deep. Immediately below this comes fresh *Sphagnum* peat, mainly composed of *S. medium*, but occasionally of *S. papillosum*. These species, both belonging to the section *Inophloeae*, are perhaps the most important peat-builders of the still unspoiled blanket bogs and raised

bogs of the British Isles, and *Sphagnum medium* is a highly important component of the 'muskegs' or acid bogs of the northern United States and Canada.

(b) *The north-western flush*

This is considerably different from the main flush. In the first place it has two clearly distinct facies. One of these is dominated by *Juncus effusus*; it has a peat depth of not more than 1.5 m. and lies at the foot of the low ridge, called Friar's Ridge, which carries dense *Calluna* growing directly on mineral soil. The other facies lies on deeper peat and has an abundance of *Eriophorum angustifolium*, which makes it comparable with the main flush. *Deschampsia flexuosa*, however, instead of occupying a marginal zone, here grows right across the area.

The *Juncus* dominated region is clearly a flush in the narrower sense of the word, which implies the influence of base-rich waters draining from mineral soil and rock. As Table 1

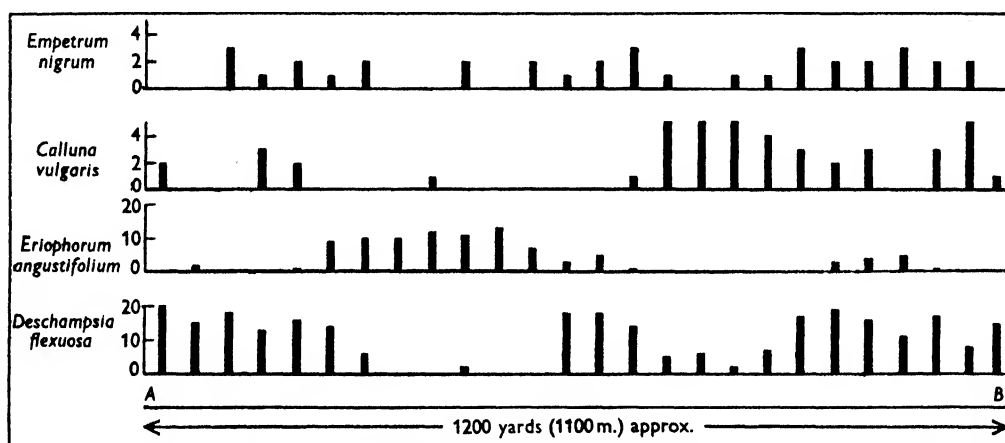


Fig. 2. Distribution of the main species along the transect AB. Explanation is given in the text.

shows, the plant community is rich in species compared with the general bog surface. Some of the species, such as *Anthoxanthum odoratum*, may well have been brought in by the sheep which wander up the relatively dry banks of Burbage Brook to seek the sweeter grazing provided by this corner of the bog. The table shows frequencies for two groups of quadrats, one taken where *Juncus effusus* was dominant, the other taken in patches in which this species was scanty. Such patches were scattered about through the area. pH values taken in the Juncetum were markedly higher than any recorded for any other part of the bog. Five samples scattered through the area gave values of 4.13, 4.64, 5.24, 5.35 and 5.70.

The other facies is not clearly dominated by any one species, for although *Eriophorum vaginatum* is almost everywhere present, it does not form large or conspicuous tussocks. *Sphagnum recurvum* occurs frequently and looks healthy; it may be locally dominant in patches up to 50 cm. in diameter. *S. fimbriatum* is of common occurrence, and *S. plumulosum* is found occasionally. *Oxycoccus quadripetalus* is much more abundant in this community than elsewhere on the bog.

Another striking difference from the main flush is found on digging below the surface. The subsurface peat, down to a depth of 60 cm. or more, consists of *Sphagnum recurvum*

with some *Eriophorum angustifolium*, and small amounts of *E. vaginatum*. There is no well-defined layer of *E. vaginatum* peat at the surface, in fact, no abrupt change of peat type at all near the surface, and no sphagna of the section *Inophloea*. In fact, if it were not for the abundance of *Deschampsia flexuosa*, and perhaps a slight increase in importance of *Eriophorum vaginatum*, in the actual live surface, we might consider the latter as representing closely the vegetation which has built up the uppermost 60 cm. of the peat of this area—which, in other words, has been growing there for the last 800 years* or more. The *Deschampsia* cover is entirely superficial, though it must have been in existence for long enough to leave a network of dead rhizomes below the living mat. This tough blackish network binds together the upper surface of the peat.

Fig 3 shows data for the transect *CD*, constructed exactly as described for Fig. 2. It shows clearly the difference between the two flushes with regard to the behaviour of *D. flexuosa*. It shows also the complete dominance of *Calluna* in the watershed region

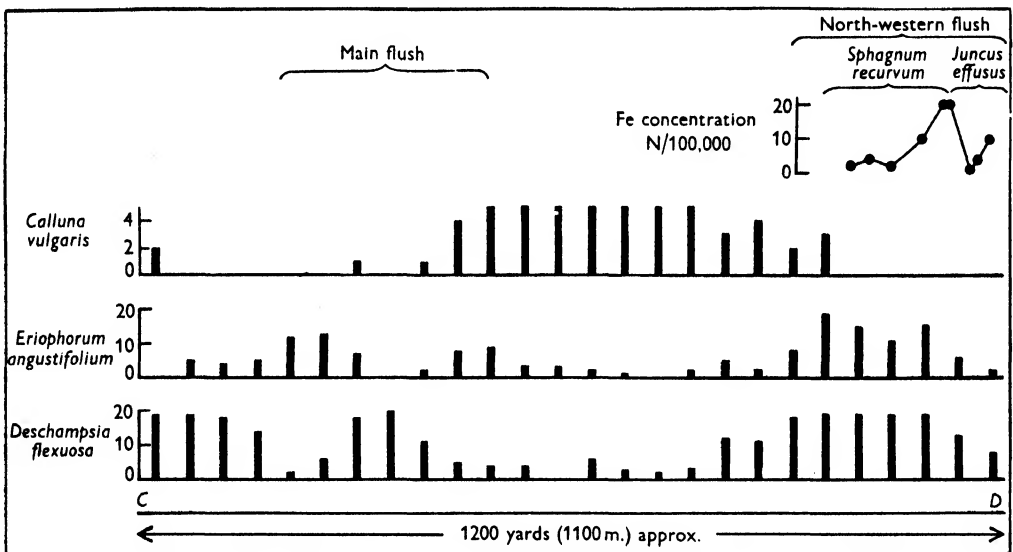


Fig. 3. Distribution of the main species along transect *CD*, and results of tests for iron salts at certain points along the transect.

between the two flushes. In this area, as illustrated by the frequency figures in Table 1, *Eriophorum vaginatum* is the only abundant phanerogamic associate. *Empetrum nigrum* was only present in five out of the 130 quadrats which lay along this line.

In addition to the data on species, this diagram gives the results of tests made at certain points along the line, to determine roughly the content of iron salts in the soil water. The streams running off the bog are obviously rich in iron salts, and it seemed likely that tests for iron might indicate areas which were particularly affected by water derived by run-off or seepage from the surrounding rocks. The method used was that described by Pearsall (1930). A reddish coloration is produced by the reaction of the iron compounds with potassium thiocyanate. The colour is matched against a set of colour standards made by carrying out the tests with solutions containing known concentrations of ferrous sulphate. A point of some importance in the use of this method is that the colours take some hours to develop fully, though once developed, they remain stable for days.

* This very rough estimate is based on stratigraphical data.

Fig. 3 shows that the peak values for iron content occur at the junction between the Juncetum and the *Deschampsia-Eriophorum* area. It had previously been noticed that over a belt of about 20–30 m. in width, immediately outside the *Juncus* zone, *Eriophorum angustifolium* became truly dominant, to the exclusion of *E. vaginatum*. One may reasonably suggest that these two facts are causally connected, since maximum values of soluble iron salts are likely to be associated with maximal, even if small, amounts of other soluble mineral salts, and hence this zone would favour the one of the two species which is generally recognized as more eutrophic as well as more tolerant of submersion.

The values for iron salts fall off fairly quickly from the maximum, and the three values from the central part of the *Deschampsia-Eriophorum* zone are exactly the same as those for three samples taken on the same day from places in the centre of the main flush. These values are, namely, $2N \times 10^{-5}$, $2N \times 10^{-5}$, and $4N \times 10^{-5}$. The pH values in the *Deschampsia-Eriophorum* area are also much lower than in the Juncetum, since five samples gave a mean of 3.72, with a range from 3.56 to 3.82. This is close to the mean value of 3.63 for five samples taken on the same day from the main flush; the two means are not significantly different.

These data would suggest that as far as acidity and base status is concerned there is little difference between the two flush areas, if we leave the Juncetum out of account. Nevertheless, the facts of the vegetational differences do suggest that the whole of the north-western flush has been, and still is, more under the influence of telluric water than the main flush, and that the tests applied have been too crude to reveal the causal chemical difference. Such a conclusion is suggested, for instance, by the presence of *Sphagnum fimbriatum* on the present surface of the north-western flush, and by the difference between the subsurface species of *Sphagna* in the two flushes. It is in any case a probable consequence of the difference in position of the two flushes, for the main flush, being more centrally placed, will be more effectively screened from telluric influence.

(c) Other features of the vegetation

An interesting strip of bog lies along the foot of the north boundary ridge. It is characterized in places by an abundance of *Eriophorum angustifolium*, and though it is not visibly at a lower level than the adjacent bog surface, it seems wetter, and in certain patches of it, *Sphagna* are truly dominant. The *Sphagnum* is mainly *S. recurvum*, but *S. plumulosum* occurs, and there is at least one patch with *S. papillosum* as the dominant. In these patches, *Oxycoccus quadripetalus* is abundant, and one plant of *Drosera rotundifolia* was found. This part of the bog is probably the most remote from trackways frequented by gamekeepers, shepherds, or hikers, or by sheep, and it is therefore not surprising that we should find in this area a vegetation type which is less extremely altered from the type of surface which must at one time have covered a large part of the bog.

A number of minor flush areas lie at the heads of the small tributaries of Burbage and East Brooks. They may be picked out in the field, and also in Fig. 1, by the fact that they carry abundant *Deschampsia flexuosa*. This is associated with *Eriophorum vaginatum* tussocks which are tall and vigorous, and though *E. angustifolium* may occasionally be present, it is not particularly characteristic. Fig. 4 gives the results for the short transect line EF, which crosses two such minor flush areas. The tall luxuriant tussocks of *E. vaginatum* are very characteristic, not only on this bog, but generally in the southern Pennines,

of boggy areas with a slope just sufficient to prevent stagnation of the surface water, yet not sufficient to produce conditions suitable for the invasion of *Calluna*.

Reference has been made already to the complete dominance of *Calluna* over the south-western sector of the bog, and from thence north-eastward along the watershed between the major flush areas. Over most of this zone, and again on the eastern boundary of the bog, the appearance of the *Calluna* cover may be ascribed to the periodic burning which is practised. Burning can probably be effective only where drainage conditions are already suitable for healthy growth of *Calluna*, and hence it serves mainly to increase the dominance of this species at the expense of its normal associates.

Empetrum nigrum was not recorded at all in the quadrats of transect *EF*, and general observations show that it is common only in the eastern and northern parts of the bog. For this, no obvious explanation comes to mind, but it is perhaps sensitive to burning, or at any rate not able to compete with *Calluna* when the latter is encouraged by appropriate burning practices.

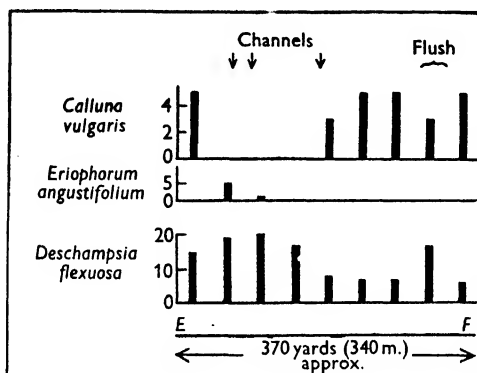


Fig. 4. Distribution of the main species along transect *EF*.

2. WATER-TABLE LEVELS AND THE DRAINAGE CHANNELS

Ringlow bog is one of the few peat-covered areas near Sheffield in which the water-table is still at or close to the surface of the peat. As we shall see, there are indications that the processes of lowering of water-table, and hence of bog degeneration, have begun here too, and are likely to continue, and we may therefore find facts here which will be significant in any consideration of the fully degenerated peat bogs of the Pennines and the highland region of Britain as a whole.

Casual inspection of the bog suggests that differences in water-table levels and ranges of variation are a major influence in determining the distribution of the vegetation types, and observations were made to test this view by taking readings of water-levels in small pits dug in various parts of the bog. In Fig. 5 are shown the results of a short series of readings beginning in the latter part of 1944, but with most of the readings confined to 1945. The water-level pits which gave these readings were in two sets of three, one set at site S towards the upper (north-eastern) end of the north-western flush, the other at site T in the centre of the south-western *Calluna* area. The three pits of a set were within an area of 9 m.sq., and they were placed so that the zero mark for each pit should be at the average soil-level. In the *Calluna* area this judgement was hard to make, and the results clearly indicate systematic differences between the three pits of a set. Nevertheless, it is

obvious from Fig. 5 that the water-table is liable to fall much farther below the surface in the *Calluna* area than in the flush area.

A longer series from the other end of the bog gave the results shown in the lower half of Fig. 7, and these again require little comment. The results were given by three pits, one (site R) in the centre of the main flush, another (site P) in the *Calluna* region of the eastern end of the bog, the third (site Z) on the south of the road on the gentle hillside slope where the peat is about 1 m. deep. This latter site is comparable with site H which gave the pollen diagram shown in Fig. 10 of the first part of this paper. The data show that there are clear differences in average water-level between the three sites, and that sometimes, though not

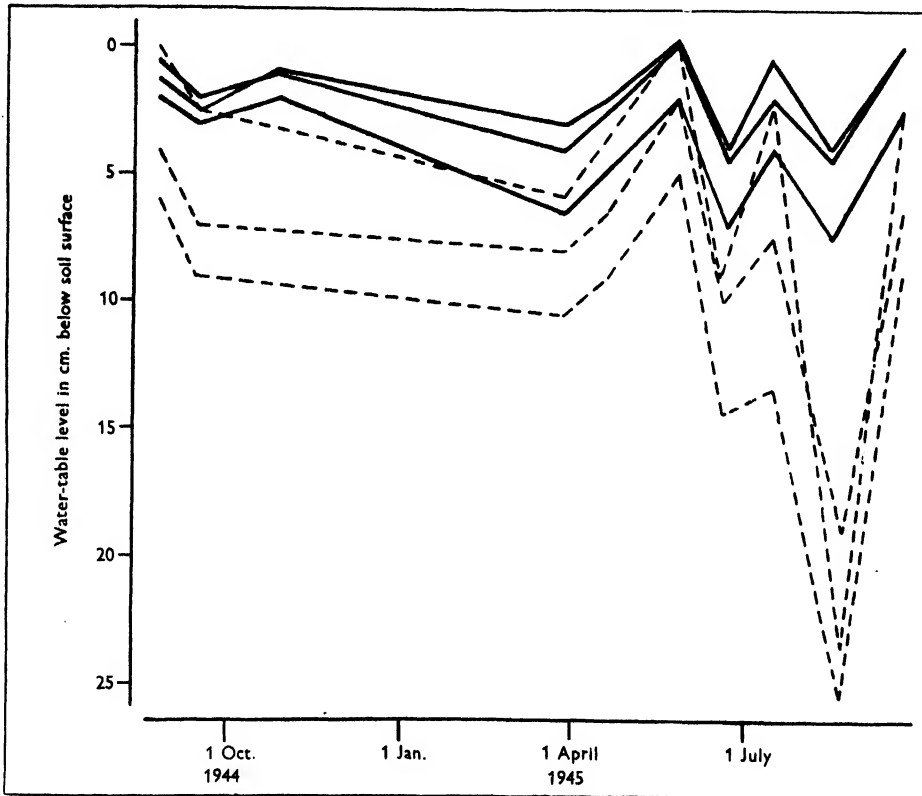


Fig. 5. Water-table levels in three pits at site S in the north-western flush (full lines) and three pits at site T in the south-western Callunetum (dotted lines).

always, site P has a bigger fall in water-table than site R in any particular dry period. Site Z, surprisingly, shows a smaller range. This is probably due to the fact that the peat is very highly humified, compact and impervious. Heavy rainfall probably runs down the surface slope, and movement of water by percolation is probably very slow, whether it is downward movement by gravity or upward movement induced by surface evaporation and transpiration.

The natural drainage channels of the bog all drain towards the south-west corner of the bog, with the exception of one or two small 'overflows' across local gaps in the eastern watershed. Drainage at the western end of the bog must therefore have been relatively better throughout most of the life of the bog, and *Calluna* has always been more favoured

at that end, a fact demonstrated by the stratigraphy. It is clear, however, that the effectiveness of the natural drainage has been continually increased because the streams have cut back secondarily into the bog after considerable depths of peat had been formed. This point was discussed at rather more length in Part I of this paper. Inspection shows that this cutting back is going on actively to-day, and also that the process is initiated by the formation of subterranean channels. Over much of the bog, the *Sphagnum* peat formed in sub-Atlantic times is soft and fluid. The existence of a visible drainage channel constitutes a breach of the peat mass as a whole, and it is easy to understand how the fluid subsurface will flow out into the breach from beneath the firm surface mat that is formed by the dominant *Eriophorum vaginatum*. This mat itself, however, in the end breaks and sinks when its support has washed away; thus a new length of visible channel is formed and so the process continues. The region immediately beyond the apparent ending of a stream tributary is often treacherous to walk over because of the hidden channel which may lurk between two solid-looking cotton-grass tussocks. In one place there is indeed a large sink-hole some 5 ft. in diameter, and 7 or 8 ft. deep.

The most important system of artificial drains is that which has been cut at the eastern end of the bog, and extends eastwards down the slope towards the village of Ringinglow. Some small cuts in the western end of the bog are indicated in Fig. 1, but they are not of particular importance. The eastern drains, on the other hand, are extensive, and must have been broad and deep when first cut. It has so far proved impossible to find out the date at which these cuts were made. Neither documents nor local inquiries have yielded any information, and this in itself suggests that the drains are old. This idea is further confirmed by the fact that they are almost everywhere choked with vegetation. The narrower ones are overgrown by heather and the wider ones are blocked at frequent intervals by dense growths, mainly of *Eriophorum* spp. Though no doubt some movement of water does occur in them, this is never fast enough to be seen.

3. pH VALUES

A few pH measurements for the western end of the bog have been dealt with already, but the main body of data comes from the eastern end. Samples for testing were collected from the three sites P, R and Z, where the water-level pits were placed. Three samples were taken from each of the three sites at every visit; the peat was collected from just below the surface, i.e. roughly at 10 cm. depth. They were packed tightly into airtight tins, brought back to the laboratory as quickly as possible, and the pH measurements carried out in the course of the next 2 or 3 hr. The measurements were made by the quinhydrone electrode method, since this had been used by Pearsall on a number of bogs and moors, and comparison with his results was desirable. During one part of the period of observations, a fourth sample was taken from each site and treated with toluol to find out whether untreated samples were likely to be undergoing changes in acidity during the time between collection and measurement. Drifts towards increased acidity had been observed when peat samples of this sort had been kept for some days, and there was therefore a possibility of error. From the full table of data given in the Appendix, it may be seen that the toluol samples tended to give values at the upper end of, or just beyond, the range of values of the untreated samples. This was, however, by no means always the case, and the error, if it existed, appeared to be very slight. To reduce it still further, if possible, during the last year of observations, the tins containing the samples were brought home in a well-lagged

box. The soil temperature in the field was measured and the temperature of the peat in each tin was measured immediately before taking the pH reading, so that it should be possible to judge whether temperature changes could have seriously affected the chemical equilibrium in the peat.

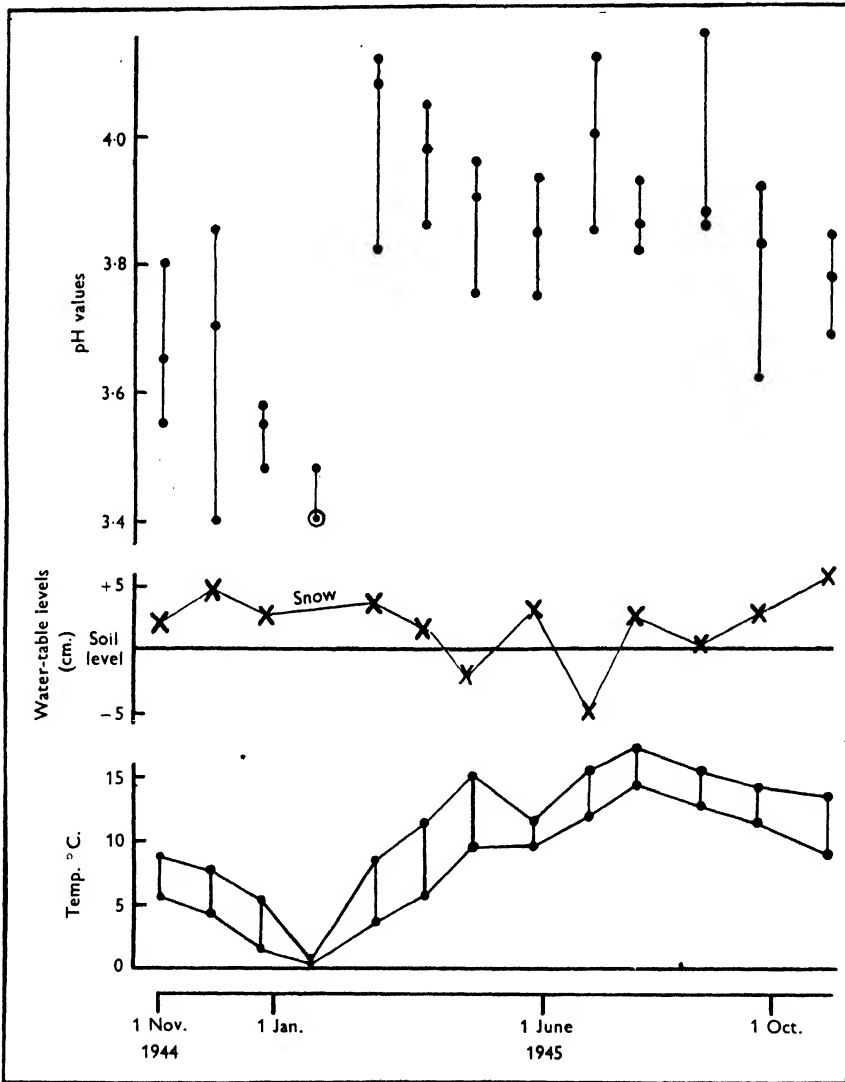


Fig. 6. Above, pH values for sets of three samples from site R in the main flush, taken every 4 weeks. Middle, water-table levels in the pit at site R. Below, the temperature changes which might be suffered by the samples between collection and pH measurement. The lower point on each date gives the soil temperature at time of collection, the upper point the temperature of the last of the three samples to be tested in the laboratory, at the time of testing.

A part of the data for this last year is given in Fig. 6, which shows the temperature measurements just described, and gives an idea of the range of variation in pH exhibited by presumably equivalent samples taken over an area of not more than 20 m.sq. The lower points on the temperature graph give the soil temperature at the time of collection; each

corresponding point on the upper line gives the temperature of the last of the three samples to be dealt with in the laboratory. Thus the vertical height of the band indicates the maximum temperature change to which the samples could have been subjected between collection and pH measurement. The largest of these maximum values was 6° C., and the average change for an individual sample was of course much less.

In spite of the wide range of variation, the diagram clearly indicates a difference in general level of pH values as between winter and summer, and it also indicates that this difference cannot be ascribed to a change in the general level of the water-table. The corresponding measurements of temperature and pH for sites P and Z gave closely comparable results to those shown in Fig. 6.

Three whole years, though not three consecutive years, are covered with varying degrees of thoroughness by the results shown in Fig. 7. Here the mean values are given for each set of three samples from each site. It is apparent from the figure that the values for site R, the centre of the main flush, are higher, taken as a whole, than those for the other two sites. Comparison with the water-table data will show that this result falls in with the conclusion reached by Pearsall (1938) that acidity is likely to be increased when the water-table on a bog falls low enough to allow oxidizing conditions to occur in the upper peat layers.

We may go further with the comparison with Pearsall's data by considering the general levels of the pH values, and it will shorten and clarify the discussion to set out the figures as follows:

Ringinglow data:

General range	3.1-4.0
Mean values of all measurements:	
Site R (<i>Eriophoretum</i> over <i>Sphagnum</i> peat)	3.71
Site P (<i>Calluna</i> over <i>Sphagnum</i> peat)	3.51
Site Z (mixed <i>Calluna-Eriophorum vaginatum</i> on humified peat on sloping ground)	3.54

Pearsall's data (page and table number refer to Pearsall (1938)):

(1) *Cotton-grass moors in Yorkshire* (mostly in the southern Pennines). All cotton-grass peat, and likely to be under the influence of erosion. Samples 15, 18, 19, 20, 23, 27, 28, 32, 40, 41 and 42 (Table 2). Mean 3.21 (highest individual value 3.44).

(2) *Moors with Calluna and Eriophorum vaginatum co-dominant*. From North Yorkshire. Samples 59-67 inclusive (Table 3). Mean 3.60.

(3) *Unmodified raised bogs in Solway* (p. 311). Glasston Moss: mean 3.64. Raeburn Moss: mean 3.46.

(4) *Modified raised bogs, with E. vaginatum over Sphagnum peat*. Samples 96, 104, 119 and 124 (Table V). Mean 3.58.

(5) *Stainmore bogs* (Pearsall, 1941). Range for unmodified *Sphagnum* bog (type A): 3.72-4.01. Range for types with *Eriophorum vaginatum* abundant 3.31-3.84.

It is obvious from these figures that as far as acidity range is concerned, the affinities of Ringinglow bog are with the more northerly bog types, rather than with the much more acid 'cotton-grass moors' of the southern Pennines. This conclusion is fortified when it is remembered that most of Pearsall's values were probably obtained during the summer

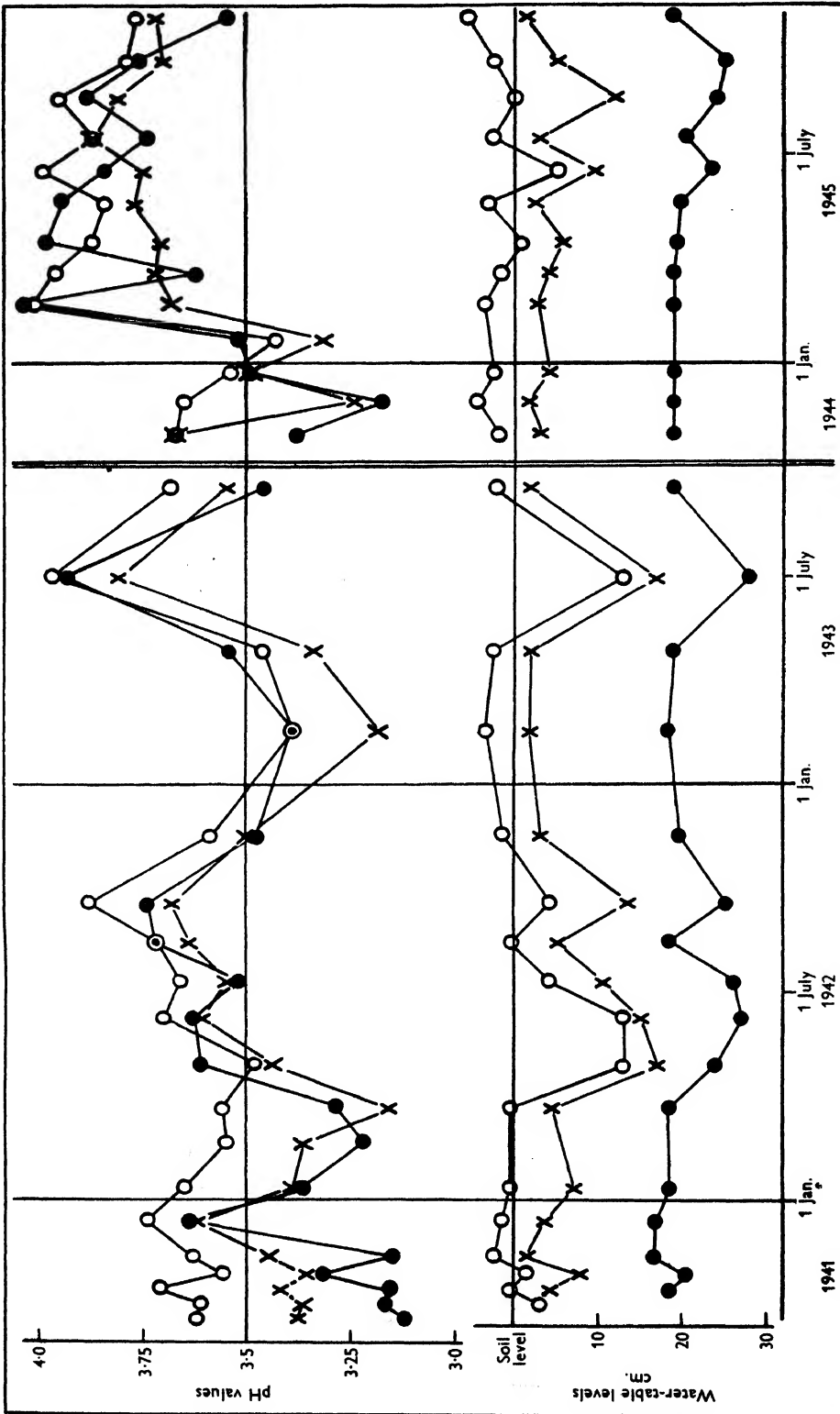


Fig. 7. Above, pH values for site R in the main flush (open circles), site P in the eastern Callunetum (crosses), and site Z on the hillside above the bog (black circles). Each value is the mean for three samples. Below, water-levels in the pits at these sites, with the corresponding symbols.

months (though this is only stated for the Stainmore data), and that the Ringinglow means would be higher if the winter values were omitted.

Thus the pH values at Ringinglow agree with those of *Sphagnum* bogs which have undergone some degree of modification so that *Eriophorum vaginatum* has become dominant, or co-dominant with *Calluna*. Moreover, they are as high as those of the unmodified Solway mosses, and only very slightly lower than those of the unmodified Stainmore bogs. They are not nearly so low as those found on cotton-grass areas where the peat is formed from cotton-grass, in other words, areas in which surface oxidation has always been prominent, though it may well have been emphasized further by erosion and hence better drainage.

Considerable importance attaches to the fact that the Ringinglow acidities are definitely not greater than those found in the corresponding vegetation types farther north in regions far removed from the influence of industrial smoke pollution. It has been frequently suggested that the high acidities recorded from south Pennine peats must be ascribed mainly to this pollution factor. The present data suggest rather strongly that this is not the case, although this question will arise again in a moment. Rather do they bear out Pearsall's conclusion that the acidity of a bog surface is a measure, roughly, of the oxidation intensity, and hence of the effectiveness of the drainage factor. The better the drainage of a peat area, the more acid will be the surface peat, whether the drainage be due to the natural topography, or to human interference of various sorts, direct or indirect.

Another point arising from Fig. 7 is the obvious seasonal rhythm in the pH values, which are higher in summer than in winter. This is the reverse of the rhythm which has been recorded by other workers, as, for example, Baker & Clapham (1939). Since their results were for mineral soils a contrast of this kind is not very surprising. The explanation very probably lies in the microbiological activities of the peat, a subject which has fallen outside the scope of the present study. There is, however, another possibility which arises from a consideration of the smoke-pollution problem. The smoke pollution is of course worse in winter, and it seems possible that winter rainfall might pick up the heavier share of atmospheric acids (particularly sulphur acids) and so bring about an increased soil acidity. To test this idea, samples of the rain water falling on the bog were collected during the winter months and gave pH values as follows:

22. iii. 45	4.65	22. ix. 45	3.62	22. xii. 48	4.25
18. iv. 45	4.28	6. xii. 48	4.09	1. ii. 49	4.92

These values clearly lie well at the upper end of the general range of the soil pH values, and it therefore seems unlikely that winter rainfall is exerting a strongly depressant effect on the pH of the soil.

4. ATMOSPHERIC SMOKE POLLUTION

There is no need to labour the point that the southern Pennines suffer from the smoke of the industrial areas. The effect of the smoke may well be of profound importance ecologically, and it is essential to have some quantitative knowledge about the problem. Luckily a good deal of information may be found, both in the publications of the Department of Scientific and Industrial Research, and in the *Reports* of the Sheffield, Rotherham and District Smoke Abatement Committee. During the nineteen-thirties, a number of measurements were being made by the Sheffield Smoke Inspectors, and these included determinations of the sulphur dioxide content of the atmosphere. Two methods were used

for this. The first, or volumetric method, consisted essentially of extracting and determining all the SO_2 from a known volume of the atmosphere. The amount of equipment needed for this method meant that it was only used at one station, namely, the centre of Sheffield. The other, or lead peroxide method, employs the capacity of a paste of lead peroxide to absorb the SO_2 from the air that surrounds it. The paste is applied to a cylinder, which may be exposed in any desired spot, with suitable protection from weather damage, and left for periods of a month or more according to convenience. The method is discussed in the D.S.I.R. *Reports* for 1934 and 1935.

It seemed that the second of these methods could be applied to the ecological problem under consideration, and accordingly two stations were set up for the exposure of lead peroxide cylinders. One was on the centre of Ringinglow bog, the other at the head of Swynt clough, near the south end of Alport Dale, a valley cut through the south side of the Bleaklow massif. This second site, though not actually on the main South Pennine watershed, is not sheltered by any mountain height from the full force of the prevailing westerly winds. The cylinders were exposed for two months at a time. After exposure, the cylinders were analysed by Mr A. O. Jones in the laboratories of the Sheffield City Analyst,

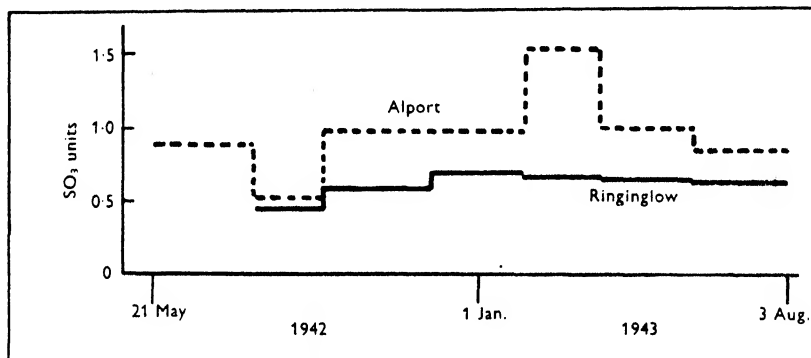


Fig. 8. Results of estimations of sulphur dioxide content of the air by the lead peroxide method.

who also carried out the same analyses for the Sheffield Smoke Inspectors. The results for Ringinglow and Alport are therefore strictly comparable, as far as technique is concerned, with the results given in the Sheffield Smoke Committee's *Reports*.

The results of the analyses are expressed in mg. of SO_3 per sq.dm. of exposed surface per day, and this is what is meant by the 'SO₃ units' which are plotted in Fig. 8. It is clear from this figure that the results are higher for the Alport site than for Ringinglow, which may seem surprising, since Alport lies 14½ miles (23 km.) from the centre of Sheffield, Ringinglow only 6½ miles (10.5 km.). Alport, on the other hand, is only 19 miles from the centre of Manchester, and only 6 and 6½ miles respectively from Hayfield and Glossop, which lie at the eastern edge of the south Lancashire industrial area. Bearing in mind the preponderance of westerly winds, the result becomes readily understandable.

Let us now compare the Ringinglow and Alport results with some taken from the Sheffield, Rotherham and District Smoke Abatement Committee's *Reports*. The figures give the approximate annual range of recorded SO_3 units, as defined above.

	Min.	Max.
Alport, 14½ miles west of Sheffield City centre	0.5	1.5
Ewden, 8 miles north-west of Sheffield City centre	0.5	1.6
Ringinglow, 6½ miles west-south-west of Sheffield City centre	0.4	0.7
Dore, 5 miles south-west of Sheffield City centre	0.4	2.0
Surrey Street, at the city centre	1.3	6.0

These figures suggest a steep gradient in the smoke pollution from the city centre to the outskirts, but a much less steep gradient from the outskirts to the distant rural areas. It must be noted, however, that the Ringinglow and Alport data are for years during the war, when smoke abatement measures were not enforced, whereas the other figures are for pre-war years. Hence the wartime figures may be somewhat too high relative to the others. Be this as it may, it is clear that sulphur dioxide may be found in the atmosphere all over the country that lies between Manchester and Sheffield, and that the amount occurring over Ringinglow bog is of the general order expressed by the figure of 0.5 SO_3 unit. This figure can be roughly translated into a quantity which conveys more meaning.

The *Report* for the year 1934 gives a figure which brings out the strong parallelism between SO_2 concentrations measured volumetrically and SO_3 units measured by the lead peroxide method. It can be judged from the figure that over the ranges of 1.3–7.0 SO_3 units and 80–300 parts of SO_2 per 10^6 parts, the relationship is approximately linear. Our figure of 0.5 SO_3 unit lies outside the range, and at low values the linear relation may not hold; however, as a rough estimate, 0.5 SO_3 unit is equivalent to 50 parts per 10^6 of SO_2 in the atmosphere.

Suppose now that in the space of time of say 2 days, 2 cm. of rain falls from an average height of 500 m. and in so doing removes all the SO_2 from the air through which it falls; if we use the value just given for the SO_2 concentration, we can calculate that the pH of the rain falling on the surface will be 4.0. This estimate would be lower if a greater height of origin of rain were assumed, and a lesser fall of rain were assumed to be able to remove all the sulphur dioxide. Even assuming a fall of 1 cm. of rain through 1000 m., however, does not bring the calculated value below 3.3. There is thus a fairly good correspondence between these calculations and the actual measurements of rain-water pH made at Ringinglow. There is agreement also with the observed values for pH of rain water that are given in the D.S.I.R. *Report* for 1939 for instance. These data show that in industrial areas, the values range roughly from 3.7 to 4.0, with lower values very rare, and values below 3.0 never recorded.

Although no observations were made on aspects of smoke pollution other than sulphur dioxide concentrations, it is possible to derive some estimate for the fall of solid matter, mainly in the form of soot, from the existing data for Dore and Ewden. There is generally a fairly close correlation between SO_2 measurements and solid matter deposits, and since Dore and Ewden both give SO_2 figures rather higher than Ringinglow, it is reasonable to assume that solid matter figures for these two sites will represent the upper limit for what is likely to be deposited at Ringinglow. The average figure for both Dore and Ewden is about 8.5 tons per sq. mile per month, or roughly 0.4 g. per sq.m. per month.

Even though the Ringinglow average is probably less than this figure, it is not surprising that the sheep are grey, and that slides made from the surface peat for pollen counting are almost unusable on account of the soot density. It seemed possible that something could be found out about the 'soot effect' in relation to the vegetation, by tracing the depth to which soot could be detected. For this purpose, columns of peat were collected, which were about 100 sq.cm. in cross-section, and extended from the surface down to 15 or 20 cm. from the surface. They were transported intact to the laboratory, and there each in turn was cut open down the centre with a razor as cleanly and quickly as possible. When first exposed, such a surface frequently exhibits marked colour changes from one level of the peat to another, but the access of air quickly darkens the lighter colours, so that the

the peat than it is farther down. This could be due to at least two causes. First, and very probably, the output of smoke, whether industrial or domestic, may have been at a much higher rate in the last thirty or forty years than previously. Secondly, the rate of peat growth may have been much slower during the formation of the uppermost 2 cm. At present there seems little evidence bearing on this latter point.

5. INTERPRETATION AND DISCUSSION

It has been shown that the greater part of the peat mass has been formed by a vegetation which was dominated by species of *Sphagnum*, but that there has been modification of the surface so that at present only *S. recurvum* is present in any quantity, and only over a small proportion of the area. From data given in Part I of this paper, it appeared that the loss of *Sphagnum* from the south-western part of the bog, now dominated by *Calluna*, took place considerably earlier than from the eastern end. At the south-western end the loss was likely to have begun some 700 or 800 years ago and was ascribed tentatively to the greatly increased drainage caused by the cutting back of the streams belonging to the natural drainage system.

At the eastern end, however, the date of the change seems likely to have been about 100–150 years ago, judging both by the pollen diagram and the data on soot deposition. In view of the writer, this change is also attributable to changed drainage relations, but before discussing this, it will be useful to discuss the view that has been put forward from time to time, according to which the dominance of *Eriophorum vaginatum* over many areas of the south Pennine moors is due to that species being tolerant of atmospheric smoke pollution, whereas the previous dominants are not. This hypothesis cannot be excluded on the existing data; on the other hand, there are reasons against accepting it until some positive evidence for it should come to light. The direct evidence so far obtained has been shown to be, if anything, very slightly against the hypothesis. There is, however, a much stronger ground for not accepting it at this stage, though here it is not a matter of direct evidence. The objection lies in the fact that the degradation of *Sphagnum* bogs is a phenomenon characteristic of *all* the highland region of the British Isles, and not at all confined to those parts which lie in the centre of densely populated industrial districts. Whether we are in the Argyll highlands, the Lake District, the northern Pennines, Wales, or Dartmoor, we can readily find examples of the replacement of *Sphagnum* dominance by that of *Calluna*, of *Scirpus caespitosus*, and, most commonly of all, of *Eriophorum vaginatum*. It will surely be more satisfactory to find some general explanation that will apply to all these diverse areas, and also to the southern Pennines, rather than to accept an explanation for the southern Pennines which could not possibly apply to any of the rest of the highland region.

This is not the place to discuss the general problem, but it is perhaps permissible to anticipate later publications to the extent of saying that the most likely general explanation is that which may be summed up in the phrase 'changed drainage relations'. This would not exclude the idea—it would in fact depend on it—that the change in drainage could be due to somewhat different factors in different stretches of bog; such factors might in some cases be 'natural', in other cases due to human activities of various sorts.

In view of what has just been said, we may return to the problem in hand, namely, the surface of Ringinglow bog, and re-emphasize the affinity which has been demonstrated

between it and the modified *Sphagnum* bogs occurring farther north, more especially those of the Stainmore region, an affinity both of surface cover and acidity range.

The increase of *Calluna* at the south-western end of the bog has already been attributed to the slow headward extension of the natural drainage system, and further encouragement by burning. Over the south-eastern quarter of the bog we are dealing, surely, with the sudden effects of the cutting of the artificial drains. The lowering of the water-table immediately around the drains was sufficient to induce the dominance of *Calluna*, and this has been maintained in spite of the subsequent infilling of the drains by vegetation. Farther afield the lowering of water-table gave optimal conditions—so the interpretation runs—for the growth of *Eriophorum vaginatum*. It appears that water-level conditions are not, however, optimal at the present day, but that the increased wetness, due to the poor functioning of the drains, has encouraged *E. angustifolium*.

Both *Calluna* and *Eriophorum* are components of normal undisturbed *Sphagnum* bog communities, and their remains are demonstrable in the *Sphagnum* peat of Ringinglow bog. It is not surprising therefore that a sudden change of water-level should bring about a quick readjustment of equilibrium between the competing species of the community. In the regions of the bog more remote from immediate effects of altered drainage, where peat growth was always rather slower, and *Sphagnum* less completely dominant, and where burning has probably been less frequent, we could expect that the slight drop in water-level would bring into being just that mixture of *Calluna* and *Eriophorum vaginatum* that we do in fact find there.

On this interpretation it is easy to see why the main flush shows evidence of drastic change within the last 200 years, whereas the north-western flush does not. One feature of the vegetation, however, seems to need some additional hypothesis, and that is the abundance of *Deschampsia flexuosa* over the surface of the north-western flush. Over the rest of the bog, it seems to be abundant only in those areas in which it can colonize the tops of *Eriophorum vaginatum* tussocks where these are growing healthily in areas just too wet for invasion by *Calluna*. If invasion by *Calluna* is successful, then *Deschampsia flexuosa* is suppressed. On the north-western flush, however, *Eriophorum vaginatum* is neither dominant nor tussocky, and the only tentative hypothesis which can be offered at present is that in some exceptionally dry season during the past twenty years, it was possible for fire to spread beyond the main *Calluna* region and to create conditions for a time in the surface of the flush which were favourable to the spread of *Deschampsia flexuosa*, and that since then the species has managed to maintain itself in spite of apparently unsuitable conditions.

The evidence concerning soot deposition made it seem likely that *Eriophorum vaginatum* became dominant at the time when atmospheric smoke pollution was becoming appreciable, or slightly sooner. The date may be assumed to be not much over 150 years ago, and this would not be at all an unlikely date for the construction of the artificial drains. The evidence also suggested that the pollution rate at the present day may be much higher than it was say 100 or 150 years ago. Hence even if it is correct to hold that drainage relations were the decisive environmental factor 150 years ago, it does not follow that a return to the original conditions of water-level would induce a return of *Sphagnum* dominance. Since it appears that the centre of the main flush is at the moment too wet for healthy growth of *Eriophorum vaginatum*, the absence, in spite of this, of *Sphagnum* could well be ascribed to toxicity due to the smoke deposits. One or two points need to be borne in mind however;

one of these is that there is at least one patch of very healthy-looking *Sphagnum papillosum* growing in a central position on the bog (about half-way along transect-line *AB*). Another point is the absence of nearby *Sphagnum* colonies (other than *S. recurvum*) which could act as a source of invaders; again, the rise of water-table may have been so recent that there has been as yet no time for invasion. On this question, the future may be left to decide, particularly as it would be open to experimental approach.

One last point in interpretation requires brief treatment. On the summits of Kinder Scout and Bleaklow mountain there are deposits of peat of about 12 ft. (4 m.) in depth, the upper two-thirds of which are composed of a *Sphagnum* peat of just the same type as that which makes up the greater part of the peat at Ringinglow. The mountain-top peats are severely eroded and are therefore not live bogs at all at the present day. Why, then, has erosion been so slight in the Ringinglow peat, and why is it proceeding to-day at such a leisurely rate? To answer this at all fully would require a long discussion of the whole phenomenon of peat erosion. At present it must suffice to say that the reason seems to be a topographical one, in that the Ringinglow area is almost completely surrounded by protective slopes. In other words, the peat has been formed in an area which is predominantly concave, and has only one major drainage outlet. Only at that one point therefore will there be any tendency towards mechanical breakdown of the margin of the peat mass, owing to the fluidity of the *Sphagnum* peat. Thus only at that one point will there be an outflowing of the semi-fluid subsurface peat into the drainage channels and a cutting back of the drainage channels in the manner described elsewhere in this paper. Where the same type of peat mass has formed over the predominantly convex surface of a mountain top, there will be a tendency for mechanical breakdown all round the circumference of the bog, and hence erosion will proceed from all sides at once and produce the devastating effects that may be seen not only on Kinder Scout and Bleaklow, but in practically every area of the British Isles where deep, little humified peat has formed on convex areas of any extent.

SUMMARY

1. The vegetation of the bog may be interpreted as consisting essentially of two large flushes drained by the two streams which meet at the single main drainage outlet of the bog. *Eriophorum vaginatum*, *E. angustifolium*, and *Deschampsia flexuosa* are the most important species of the flush vegetation, except for a small area close to the bog margin, which is dominated by *Juncus effusus*. Between and around the flush areas are regions which are slightly less wet, and are characterized by abundant *Calluna vulgaris*.

2. The water-table has never been found to lie at a depth greater than 30 cm. from the soil surface, even in the best drained parts of the bog. In the wetter parts it may be above the general soil-level for large parts of the year.

3. The pH values of the peat at about 10 cm. depth range from 3.1 to 4.1, with a mean value of 3.7 for the wet flush area and 3.5 for areas with abundant *Calluna*. The values are higher in summer than in winter.

4. Some observations were made on the sulphur dioxide content of the air over the bog. The maximum values observed were about one-ninth of the maximum observed for the centre of Sheffield by other workers. It seems likely that values as high as those at Ringinglow may be found anywhere between Manchester and Sheffield.

5. The view is put forward that the bog shows strong affinities with some of the *Sphagnum* bogs from the north of England described by Pearsall, such, for example, as

Stainmore bog, especially that part of it which is now dominated by *Eriophorum vaginatum*. While the evidence does not exclude the possibility that the degradation of Ringinglow bog might have been caused by atmospheric smoke pollution, it is also possible to explain it in terms of improved drainage conditions. Thus its recent history would be in line with that of many bogs situated far away from industrial regions.

I am indebted to Mrs Withers, and latterly to the Sheffield City Corporation, for permission to work on the bog. Grateful acknowledgement is made to the administrators of the University of Sheffield Research Fund for a grant which met the cost of transport for part of the fieldwork carried out during 1948. Warm thanks are due also to Mr James Law, Chief Smoke Inspector for Sheffield, for his advice concerning the measurements of atmospheric smoke pollution, and for the loan of equipment.

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CORRIGENDUM TO PART I OF THIS PAPER

It was stated in the Appendix that the pollen of *Juncus* had been found in one of the samples of profile C. Prof. Faegri of Bergen, and Dr Iversen of Copenhagen, have been kind enough to examine one of the slides which show these pollen grains. They are of the opinion that the grains appear fresh and are therefore likely to be a contamination from some recent source. Although I cannot explain how such a contamination could have arisen, these expert opinions carry so much weight that I feel they should be published.

APPENDIX. PRIMARY pH DATA

The accompanying table gives the primary data from which were calculated the mean values plotted in Fig. 7. Figures in italics refer to samples treated with toluol, and are not included in the means. The quinhydrone apparatus was calibrated from time to time by means of standard buffer solutions.

On each date, the values for the three samples of a site are listed in the order in which they were obtained. Then if the first of the three values were always, or usually, higher than the second, and the second higher than the third, it would indicate a correlation between acidity and length of time from the collection of the sample to the measurement of pH. There is no obvious indication of such a drift in the figures in the table.

Ringinglow bog, near Sheffield

Date	R	P	Z	Date	R	P	Z	Date	R	P	Z
18. ix. 41	3.63	3.56	3.16	11. vii. 42	3.60	3.65	3.52	29. xi. 44	3.85	3.50	3.38
	3.66	3.25	3.11		3.52	3.42	3.38		3.70	3.13	3.07
	3.56	3.33	3.10		3.77	3.58	3.65		3.40	3.10	3.10
					3.77	3.77	3.68	27. xii. 44	3.55	3.50	3.48
30. ix. 41	3.66	3.35	3.18						3.58	3.58	3.60
	3.52	3.45	3.21	15. viii. 42	3.77	3.60	3.77		3.48	3.40	3.40
	3.65	3.30	3.11		3.52	3.60	3.68				
15. x. 41	3.73	3.42	3.21		3.87	3.71	3.71	23. i. 45	3.48	3.40	3.50
	3.68	3.58	3.14		4.02	3.52	3.91		3.40	3.07	3.55
	3.71	3.25	3.14	18. ix. 42	3.74	3.52	3.81		3.40	3.48	3.50
29. x. 41	3.70	3.35	3.28		3.87	3.77	3.60	24. ii. 45	3.82	3.70	4.08
	3.65	3.30	3.39		4.02	3.74	3.81		4.12	3.79	3.97
	3.52	3.42	3.28		3.84	3.81	3.65		4.08	3.55	4.05
13. xi. 41	3.70	3.45	3.21	17. xi. 42	3.60	3.67	3.42	22. iii. 45	3.98	3.80	3.50
	3.59	3.56	3.14		3.60	3.38	3.52		3.86	3.77	3.85
	3.59	3.35	3.11		3.58	3.45	3.45		4.05	3.60	3.48
					3.77	3.58	3.58	18. iv. 45	3.90	3.63	3.98
14. xii. 41	3.73	3.45	3.66						3.75	3.78	3.96
	3.77	3.65	3.59	16. ii. 43	3.50	3.12	3.60		3.96	3.72	4.00
	3.73	3.77	3.63		3.42	3.12	3.45	22. v. 45	3.75	3.90	3.90
12. i. 42	3.70	3.42	3.21		3.25	3.32	3.12		3.85	3.60	4.10
	3.59	3.25	3.27		3.42	3.45	3.35		3.93	3.82	3.82
	3.66	3.49	3.63	28. iv. 43	3.42	3.60	3.52	20. vi. 45	4.12	3.82	3.93
18. ii. 42	3.52	3.28	3.21		3.52	3.26	3.52		3.85	3.57	3.85
	3.56	3.39	3.21		3.35	3.15	3.58		4.00	3.85	3.75
	3.56	3.45	3.25		3.52	3.18	3.60	17. vii. 45	3.86	3.75	3.80
22. iii. 42	3.65	3.17	2.87	30. vi. 43	4.10	3.71	4.01		3.93	3.93	3.86
	3.53	3.00	3.50		3.94	3.87	3.87		3.82	3.93	3.57
	3.41	3.41	3.50		3.87	3.84	3.95	22. viii. 45	4.16	3.68	4.05
					4.05	3.71	3.87		3.88	3.83	3.91
29. iv. 42	3.41	3.52	3.60						3.86	3.93	3.67
	3.52	3.45	3.58	15. ix. 43	3.80	3.52	3.15	22. ix. 45	3.83	3.58	3.80
	3.50	3.35	3.65		3.62	3.42	3.42		3.62	3.80	3.77
	3.50	3.50	3.35		3.62	3.70	3.72		3.92	3.73	3.70
					3.83	3.65	3.85	30. x. 45	3.78	3.61	3.59
9. vi. 42	3.67	3.74	3.42						3.69	3.57	3.46
	3.60	3.60	3.68	1. xi. 44	3.80	3.65	3.28		3.84	3.97	3.59
	3.84	3.50	3.77		3.65	3.84	3.28				
	4.17	3.95	3.74		3.55	3.52	3.58				

NOTE

TRANSPIRATION AND WATER UPTAKE OF CUT SHOOTS

A NOTE ON AN APPARATUS FOR SIMULTANEOUS MEASUREMENTS
IN THE FIELDBY G. C. EVANS, *Botany School, University of Cambridge**(With one Figure in the Text)*

Little originality is claimed for the apparatus described below, which merely incorporates convenient features of several well-known types of potometer. Originally devised for class work, it has, however, proved very useful in the field when information has been wanted on the transpiration and water uptake of cut shoots simultaneously. As several inquiries have indicated that the information may not be generally available, it was thought that the publication of details might be of interest.

Ideally, an instrument for field observations of this kind should meet several requirements:

(1) It should be small, robust, self-contained, and portable; and it should be so arranged that there is minimal disturbance to the natural environment of the plant when it is exposed there.

(2) If it is desired to extrapolate back from the observations to the rates at the time of cutting, the apparatus must be both easy to assemble rapidly, and capable of giving frequent readings; this in turn means that the sensitiveness must be as great as possible, the practicable limit for field work being about 0.01 ml. and 0.01 g.

(3) It should contain the minimal amount of water, in order to minimize the effects of temperature changes on the volume and hence on the observations of water uptake. The apparatus to be described has a normal working volume of about 4 ml., making such interference negligible.

(4) It may, however, be necessary not only to take a series of readings over a short period but also to leave the apparatus unattended for several hours, or even overnight; provision must therefore be made for a reservoir of water sufficient for expected uptake during such an experiment. In this instance the temperature should be measured at the beginning and end of the period, and if necessary a correction should be made to the apparent change in volume.

Fig. 1 illustrates an apparatus which fulfils most of these requirements. The vertical arm *A* is a 1 or 2 ml. graduated pipette, the size chosen according to the expected rates of uptake to be measured. The horizontal arm and the vertical arm *B* are of capillary tubing of similar bore. The short vertical arm *C* is of suitable bore to contain the cut end of the shoot or petiole in use. A reservoir *D*, which may be of two alternative forms, is connected to the arm *B* with rubber tubing closed by a screw clip. *D*₂ is used for the measurement of uptake over long periods, unattended, and has an upper tube of wide capillary etched with a single mark. For each observation it is filled to the mark from a burette fitted with a long fine capillary nozzle. *D*₁ has a wide neck and can be filled by a funnel. It is accordingly used on all other occasions as being more convenient.

All the rubber tubing joints are wired; a double turn of no. 30 gauge copper has been found most satisfactory, as the first turn can be pulled really tight before twisting the ends of the second turn. It may be mentioned that some tissues are damaged by prolonged

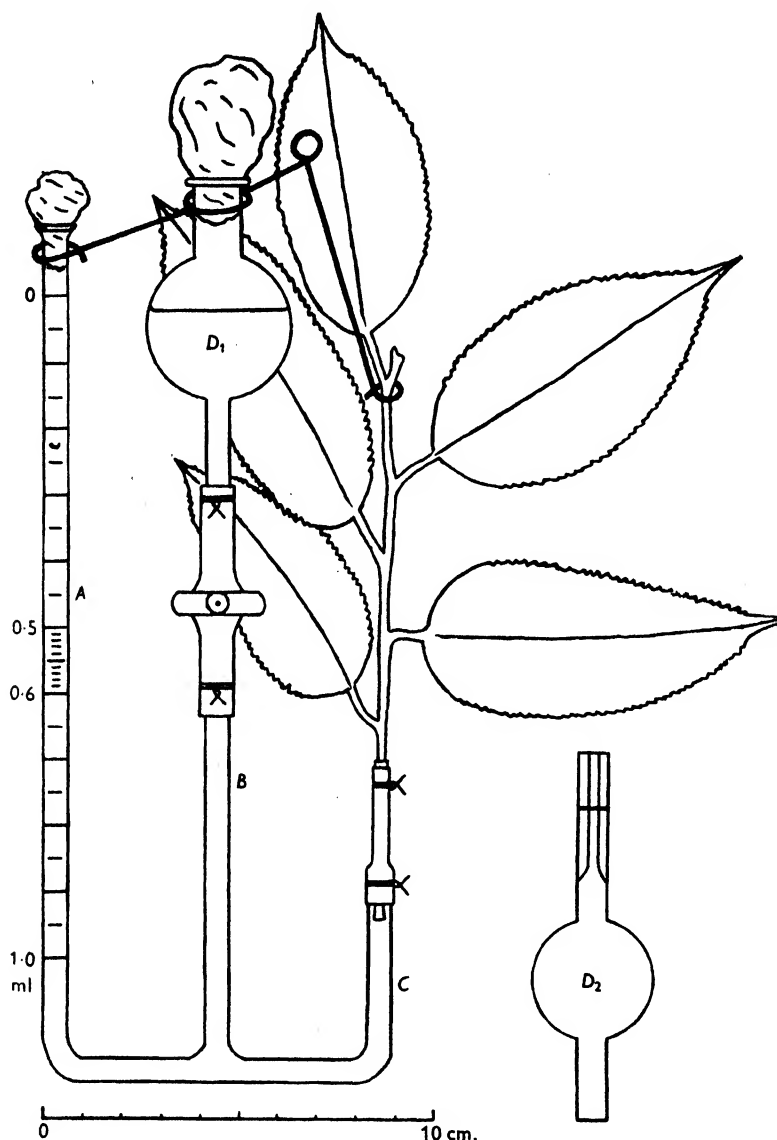


Fig. 1. An apparatus for the simultaneous measurement of the rate of transpiration and water uptake of cut shoots in the field. *A*, graduated arm reading to 0.01 ml.; *B*, connexion to reservoir; *C*, short arm of bore wide enough to contain end of cut shoot; *D*₁, reservoir for experiments with short intervals between readings; *D*₂, reservoir used when the apparatus must be left unattended for long periods.

contact with modern vulcanized rubber tubing; for this joint between the plant and arm *C* it is possible, but awkward, to use alkathene tubing; the size being carefully chosen as this material is relatively inextensible.

A rough chemical balance reading to a centigram can be used to weigh the apparatus, which when assembled seldom exceeds 100 g., but a portable case may be needed as a wind shield. A damped lever balance giving direct readings of fractions of a gram is preferable, both for its rapid reading and lower sensitivity to wind. The only other accessories normally required are a pair of small pliers, an enamel plate, a half-pint tumbler, a pint of distilled water and a scalpel or safety-razor blade.

Having assembled the potometer and wired the joints, a convenient procedure is to hang it up, fill the reservoir with water and then gently open the clip, when water should penetrate all the tubes without any inclusion of air. The joints are carefully observed for possible leakage, and the clip is then adjusted until there is a very slow leak from the open end of the rubber tubing on arm *C*. The enamel plate, full of water, is then held under the shoot to be cut off so that part bends below the water, and the stem is severed there with a sharp blade. The cut portion is trimmed under water to the desired length and inserted without including an air bubble into the water trickling from the potometer. It is then gently pushed down until the cut end shows below the rubber, and wired in. If the stem or petiole be very thin, it is sometimes necessary to slip on a piece of bicycle-valve tubing during the preliminary trimming, and this has been illustrated in Fig. 1. Surplus water is then blotted away, the clip closed, the apparatus weighed, and the volume shown in arm *A* recorded. It is then suspended for a period in the desired environmental conditions. Even when the transpiration rate is low significant changes in weight and volume can usually be observed using intervals of the order of 5 min. between observations. When the meniscus nears the bottom of arm *A*, after reading the volume it can be returned to the top by admitting water from the reservoir without altering the weight of the whole apparatus. The clip should be kept as close to the arm *B* as the elasticity of the rubber will allow in order to minimize disturbances due to accidental deformation of the rubber tubing.

If the state of turgor of the leaf or shoot is a matter of interest, it will be noticed that it is possible to work back from a determination of this at the end of the experiment to the state at any time during the observations.

REVIEWS

Henry J. Oosting. *The Study of Plant Communities: an Introduction to Plant Ecology.* 8½ × 5½ in. Pp. 390, with 190 figures and half-tone illustrations in the text. San Francisco: W. H. Freeman. 1948. Price \$4.50.

The Study of Plant Communities is a text-book for an introductory course in ecology, tested over some years by use in mimeographed form at Duke and Rutgers Universities and the Universities of Nevada, Wyoming and Missouri. It aims to answer the question 'What is ecology, and what is it good for?' An outline of its scope is given by the following extract from the preface: 'The plan, in brief, proceeds from a consideration of the nature and variation of communities to methods of distinguishing and describing them. This is followed by a discussion of the factors which limit, maintain, and modify communities both locally and regionally. Thus the interrelationships between organisms and environment are emphasized and a foundation is laid for a presentation of the concepts of succession and climax. Then the climax regions of North America become a logical consideration since they are illustrative of all that comes before. To answer the questions which must arise regarding the permanence of climax, a section is devoted to past climaxes and their study and reconstruction. Finally, the potentialities of the ecological point of view in practical considerations are emphasized by a survey of its possible and desirable applications in range management, agriculture, conservation, landscaping, forestry, and even human relations.'

Throughout the book are the marks of the experienced field ecologist: there is stress upon the value of the *permanent* quadrat, the need for extreme care in noting the location marks for such quadrats, and the advantages of systematic, as against random, sampling of a stand. There is shrewd and timely comment upon the respective roles of general survey, and description and quantitative sampling of communities. It begins: 'In this connection it should be emphasized that the early procedures of observation and reconnaissance are still of extreme importance in determining where, how, and what to sample. These activities are still a necessary part of community study although they cannot be substituted for detailed analysis. They serve to form a basis for theories or ideas that may in turn be substantiated by quantitative evidence obtained by sampling. Preliminary reconnaissance may likewise help to reduce the effort expended in sampling. No sampling should be done without a thorough knowledge of the history, physiography, and vegetation of the region as a whole. Prior to sampling, the community should have been observed repeatedly in different parts of its range and more particularly under the varying local conditions where it exists. Finally the specific stand should be observed thoroughly to determine its obvious variations, its extent, limits and transitions to contiguous communities. Then, knowing all this, together with the size of the individual plants, the strata present, and the purposes for which the sampling is to be done, one may plan his procedure in terms of the desired results, the necessary degree of accuracy, and the time available for doing the work.'

The treatment of sampling areas, in number, size and spacing, follows the lines suggested by Cain, and is more convincing than that hitherto seen in ecological texts.

The author recognizes that the differences in approach between the phytosociologists of the European tradition, and the American and English ecologists, rest upon different ideas as to the phytosociological values necessary for an adequate characterization of the community—a subject on which agreement is still lacking. Nevertheless, he deplores that the methods of the Zürich-Montpellier school have not had wider acceptance in America. Perhaps it would be fair to say that he approves the technical methods rather than the objectives of that school.

Prof. Oosting makes very clear to the student the distinction between the concrete examples of a community and the abstract idea of a community, and terms the qualities arrived at by comparison of numerous stands the 'synthetic characters' of the abstract community.

Whilst succession and climax are fully dealt with, the student is spared the confusing Clementsian concept of the vegetation complex as a mature organism developing to maturity through the sere. It is a pity that he should not also be spared the false identification of latitudinal and altitudinal zonation.

A biotic factor worth consideration, along with the introduction of alien species, is surely that of the evolutionary processes themselves, the migration, hybridization, isolation and establishment of new species in new habitats; this factor may be hard to evaluate but it is constantly present.

There is a substantial and well-illustrated chapter upon the present climax formations of North America. How accurate or sufficient it is, we must leave American ecologists to say, but the treatment of the northernmost forests seems unduly sparse. For each formation the chief operative factors are concisely given, but with such great compression it is not surprising that one should think some communities or regions dealt with too briefly.

The fields of research which help to reconstruct the vegetation of the past are indicated by a brief description of identification of macro-fossils, pollen analysis, dendrochronology and relict communities.

In a book with such excellent qualities one is sorry to find no reference to the writings of Tansley; his balanced and philosophic outlook is one of very great educational value to students, and his modifying views would enhance the benefits of their assimilation of the impulsive sweep of Clementsian doctrines. It is a great pity that ecological studies in Britain and the U.S.A. should not remain an integrated science, and it ought to be possible to embrace in the one subject at least all the work published in English. In later editions the views of Watt and Jones upon cyclic processes in the climax could be added, and whilst there is no doubt much to be said for introducing the subject by adherence to the monoclimal hypothesis, the conflict between this and the polyclimal view is a good deal more fundamental than the author would have us believe.

H. GODWIN

Wenner, Carl-Gösta. 'Pollen diagrams from Labrador: a contribution to the Quaternary geology of Newfoundland-Labrador, with comparisons between North America and Europe'. *Geografiska Annaler*.

This paper is the record of results obtained by Carl-Gösta Wenner on the expedition under the leadership of the late Prof. Väinö Tanner to the coastal region of Newfoundland-Labrador. It was undertaken in the period just before the outbreak of war, and was made by a series of short journeys from landings at different latitudes on the coast between 53° and 58° N. latitude.

The central mass of Labrador is gneissic, but is overlaid with glacial drift, most of this in turn peat-covered; the topography and soils are those of recently (and perhaps totally) glaciated country. The work of de Geer and Anteus leads to the tentative conclusion that the ice-sheet still covered Labrador at a time corresponding with the Finiglacial in Europe, and that it was largely ice-clad still at the time of the European Boreal period. Prof. Tanner and the author have sought to obtain a time-scale for the course of vegetational and geological development from the marine beaches' record of the coastal movement of land and sea. Solifluction, however, is so pronounced in the climate of Labrador that it rapidly obscures the evidence in all but the most favourable sites. The lower limit of undisturbed erratic boulders, however, gives the maximum height of marine action, and the upper limit of barnacle colonies on cliff-faces has also been employed to detect high-water of neap tides, and strand-ridges have also been used. The maximum height of former sea-level lies about 70 m. Solifluction effects are present between this level and a pronounced wash-level about 40-50 m.; below this they are replaced by effects of water movement. Tanner maintains that uplift of the Labrador coast has now nearly ceased, and the author that the coast has been at its present level for a long time.

The Labrador ocean current with its burden of melting ice must always have had a stabilizing influence upon the climate of the land; because of it temperatures vary little from north to south, but change rapidly from the coast inland. In general the climate has a continental character with some maritime tendency, and finds its counterpart near the forest limit in northern Russia. Labrador is now almost entirely deglaciated, the absence of glaciers with such low temperatures being due to low precipitation. There is evidence of recent recession of the small glaciers remaining, and there is evidence in meteorological records of recent amelioration of climate, like that observed widely elsewhere in the higher latitudes of the northern hemisphere. This operates through diminished access of polar air, as against warm 'tropical' air from the south, and it appears that the rise in temperature is accompanied by a decrease in humidity.

Labrador lies on the border between arctic tundra and boreal forest, displaying a wide transition region.

The forest is strongly conifer-dominated, with *Picea mariana* by far the commonest species. *P. canadensis*, *Abies balsamea* and *Larix laricina* occur widespread but show soil or climatic preferences. *Populus*, *Betula* and *Alnus* are represented by various species but are generally insignificant in the 'ocean of conifers'. That the tree species are so few and all reach much the same northern limits, handicaps the pollen-analytic investigations here described. Spruce, and to a smaller extent fir, extend right to the forest limit, where pine is absent. This is the same situation as that in Petschora, northern Russia, and this boundary with the tundra is evidently the zone where climatic shift will most likely be evident. A coastal tundra extends far south, but is a zone in fact, where elements of the arctic flora mix with elements of the forest undergrowth, so that it has earned the term 'pseudo-arctic'. The northern tundra consists chiefly of heath and swamp. The former may be lichen- and moss-dominated, or consist of field layers of *Empetrum hermaphroditum*, ericaceous plants, dwarf birch and willow. At intervals thickets of *Alnus viridis*, *Betula exilis* and salices occur. Wenner draws attention to the differences between the forest at its vertical limits where meeting coastal tundra, and at its horizontal limits where meeting the northern tundra; this is another instance to set against the prevalent but untrue statement that vertical plant zones repeat latitudinal ones.

The author gives reason to think that at the forest limit trees frequently succumb to drought. Wind, fire, swamping and human clearance also may affect the local extermination of this woodland.

After reporting a series of critical investigations which add substantially to the general corpus of knowledge of pollen-analytic technique, the author concludes that 'As the different methods (of preparation) seem to give similar pollen spectra, a number of different methods can be used even in analysis of a single series, as in the following instance: acetolysis of the decomposing vegetation near the surface where there is little pollen, KOH boiling of peat and mud, HF treatment of clayey soils, and separation of sandy material (by Thoulet solution).' The only correction needed is for the loss of buoyant *Sphagnum* spores in the centrifugate of the acetolysis solutions. Similarly, the author painstakingly investigates the influence of preparation method upon pollen-grain size, his conclusions generally fitting into the picture being developed by several recent workers upon the subject. He concludes that size statistics do not permit the recognition of separate species in the genus *Picea*, whilst for *Betula* it appears that small grains generally imply a northerly climate and vegetation, rather than recognizable species.

The pollen analyses embrace the non-arboreal pollen, estimated upon a basis of 100 'bladder-grains' per sample. In areas and vegetation types so little known it is of importance to be able to relate pollen spectra to vegetational composition, and a basis for such reference is provided by studies of surface catch of pollen within the existing vegetation zones. From these results several points of general interest emerge.

Peat formation occurs freely in the tundra, the surface usually bearing ericoid communities. In the woodland region *Sphagnum* bogs are prevalent. A range of mire types is encountered, like that found in Scandinavia, and of special interest are the 'Aapa' bogs found in the southern forests, and the 'Palsa' mires, in which tall mounds of *Sphagnum* peat rise by the growth within them of ice masses capable of surviving the summer season.

The author undertook the collection and examination of pollen and spores of vascular plants now growing in Labrador and sought the best methods of identifying them. He compares the pollen composition of samples taken in the various vegetational regions, with the present surface vegetation, and obtains results in general of an expected type. It will be noted that good amounts of willow, *Lycopodium selago* and high frequencies of *Betula* and *Alnus viridis* pollen characterize tundra, whilst abundant *Sphagnum* spores are usually restricted to the forest belt. It is of interest that surface samples of the tundra yield grains of *Artemisia*, *Chamaenerion* and *Viscaria alpina*.

The pollen diagrams are grouped according to latitude and elevation, and show evident parallelism in the vegetational history of the different regions. In the forest region there could be traced a lower zone of birch and alder, a middle zone of increased forest growth, and an upper zone of bog vegetation in forest surroundings. At low altitudes the paludification (the extension of *Sphagnum* mires) was very pronounced in the latest period. In the unforested north the pollen diagrams show a sequence from tundra, through tundra-forest ecotone, and back to somewhat less wooded conditions. The period of greatest forest growth is that in which three 'heath' layers formed in the peat, and these are now overlaid by unhumified wet peat, formed in the latest period. Wenner rejects the possibility of employing the stage of birch-alder, or the onset of paludification in the forests as a means of synchronization, but tentatively uses for this purpose the 'heath' layers, especially the uppermost, and the upper and lower limits of *Abies* pollen.

On this basis the boundary between the tundra and the forest periods falls at the same time (Heath layer V) in the Labrador forest region as in north Newfoundland. Diagrams from the more northern barren region are difficult to interpret, but, nevertheless, show reversion in some instances. Over the area as a whole reversion to unforested conditions is limited to areas now barren of trees, but at no great distance from the forest margin.

The phenomena of vegetational history and peat growth alike seem to indicate a post-glacial 'climatic optimum' and subsequent deterioration, comparable with what has already been established in western Europe. Taking into account also the evidence of shore-line displacement the author puts forward a tentative and plausible correlation of events on both sides of the North Atlantic. He suggests that the Pleistocene ice-sheet disappeared from the Newfoundland-Labrador coast in Finiglacial time, and inland continued to wane until final disappearance in late Boreal or early Atlantic time. This alteration was accompanied by invasion of birch-alder forest. Then followed conifer forest, which reached its greatest extension in the period regarded as the post-glacial optimum and considered as falling within sub-Boreal time. In sub-Atlantic time paludification has greatly increased. Land elevation has throughout followed a course similar to that in Scandinavia.

We look forward to the extension and elaboration of this work, with its considerable promise for the understanding of Quaternary history.

H. GODWIN

Bertil Lindquist. *Genetics in Swedish Forestry Practice.* Stockholm. Svenska skogsvårds förenings förlag. Pp. 173 with 65 figures. Waltham, Mass., U.S.A.: The Chronica Botanica Co.

Ever since the convincing demonstration by Oppermann in Denmark that our European trees show heritable variation in habit, Scandinavians have been in the forefront in contributing to our knowledge of the genetics of forest trees. They have shown, chiefly for *Pinus silvestris*, that many morphological and physiological characters are heritable; stem form, crown form, type of branching (heaviness and angle formed by the branch with the stem), rate of growth, resistance to cold and to disease. The recognition of such variation is being actively followed up by translating this knowledge into practice with all possible speed. It is the aim of this enlightened and progressive country to replace as far as possible, and as soon as possible, the slow-growing, broad-crowned, heavy-branched by the faster growing types with slender, horizontal branches and narrow crowns.

That there is a task to perform at all is due to the operation of the reverse process in the past, due partly to human agency and partly to natural. For in the past the desirable forms met consumers' needs and the forest was left to be regenerated by the inferior types. This accounts for the prevalence of forests stocked with inferior types near ancient habitations and in accessible places. But inferior types are also found at higher elevations where snow pressure and the spread of spruce have tended to eliminate the more desirable narrow crowned type.

Two general methods are being adopted. First the country is being surveyed and all forests, as producers of seed with desirable potentialities are being classified according to the proportion of desirable to undesirable stems in them. Three classes are used: plus, normal and minus. Normal and minus stands in particular, may be improved by judicious thinning.

The seed collected from certified stands is not released for general use. For the recognition of climatic races means that the trees from the seed can be grown with advantage only within a certain latitudinal and altitudinal range of its source. Langlet's diagram showing the distances to which seed transfer from source to plantation site is permissible, is reproduced.

But the seed collected from certified stands is quite inadequate to meet current and future needs. Because of this all practicable means are adopted to increase the production of desirable seed. Hence the marking and registration of élite mother trees, the application of methods of stimulating flowering and fruiting (strangulation, girdling, root pruning), the grafting of desirable scions on vigorous stocks with a good record of seed production (although these other characters may be undesirable), the establishment of nurseries of these grafts at a number of centres selected with the range of profitable growth of the climatic races in mind. In this way it is hoped to produce the necessary amount of good seed at a rate cheap enough to drive bad seed off the market.

Scots pine is the tree chiefly dealt with, but accounts are given of desirable races of spruce, birch (with different patterns of decorative timber) oak, alder, beech, etc., and an assessment made of the seed requirements in the future.

The completion of this programme would mean that at some distant date the traveller from New Zealand would survey forests of remarkable uniformity. The point had been foreseen and an effort is to be made to maintain the stock of variability by leaving certain areas of forest intact.

All this will cost money but estimates of cost are checked against estimated increased returns in quantity and quality of timber and gains in lower establishment and management costs.

The author, who is Professor of Forestry at the Royal College of Forestry, Stockholm, is very well equipped for his task. His expert knowledge of forestry, ecology and genetics is combined with perseverance, thoroughness and drive, qualities which are reflected from every page of this sound book. It was first published in Swedish in 1946 but a quick appreciation of its merits led to an early call for an English edition. The book is well and profusely illustrated. There is a useful appendix of current literature on forest tree improvement.

A. S. WATT

Riddelsdell, H. J., Hedley, G. W. and Price, W. R. (Editors on behalf of the Cotteswold Naturalists' Field Club.) *Flora of Gloucestershire*. Pp. clxxxii + 667; with coloured frontispiece, 43 half-tone plates, two maps in text and four in colour in gusset pocket. 1948. Arbroath, Scotland: T. Buncle and Co. Ltd. 42s.

This *Flora* contains much that is noteworthy in a work of its kind, and is of considerable interest to the ecologist as well as to the taxonomist. The vegetation of Gloucestershire has received comparatively little attention since the early days of ecology in this country, and we should be grateful to W. R. Price for presenting in the introduction a connected account of the plant communities of the county. It is not easy to explain concisely to the general reader (for whom the descriptions of the vegetation are partly intended), the ecological terms and principles involved in a system of successional classification. This difficulty has led, especially in the analyses of the factors responsible for the present-day distribution of vegetation, to some rather misleading statements, which might have been avoided with the assistance of a trained ecologist. Thus, in the interesting section on woodlands, Mr Price makes the following statements (although he often realizes the importance of biotic, edaphic and historical factors in other connexions): 'The average altitude therefore of the larger woods is about 570 ft. Obviously altitude is a determining factor' (p. lxiv). 'The present woodland distribution is, therefore, as the maps show, the result of position, altitude and rainfall, in other words high rainfall has been the major factor' (p. lxv). And on p. lxxix, the statement 'It is hard to believe that at this time [the Atlantic Period] the Cotswolds were not forested with woods of ash, beech and perhaps hornbeam' is not quite in accord with the view expressed by Tansley on the cited page of *The British Islands and their Vegetation*. However, the whole section in question should serve as a valuable guide and stimulus to fresh work on the fascinating problems presented by the vegetation, especially of the Cotswolds, such as the floristic richness of the beechwoods compared with those of the Chalk, and the status of the various types of oolitic grassland.

The introduction also contains accounts of the solid and superficial geology, climate, prehistoric vegetation, agriculture, changes brought about by the War in the weed flora in the parish of Ashchurch, botanical statistics, and an admirable section on the history of Botany in the county. Surface Utilization, Soil Fertility and Grasslands maps (the latter two on an agricultural basis) are reproduced from *A Survey of Gloucestershire* by permission of the County Council, and form a useful adjunct to the introduction. The more usual geological, rainfall and topographical maps are also included.

The flora proper has been carefully prepared in collaboration with specialists, and contains much interesting information. Ecologists will find the keys to certain critical species widely applicable in England; to the Batrachian *Ranunculi* by Dr R. W. Butcher, to *Ulmus* by R. Melville and H. K. Airy Shaw, to *Carex* by E. Nemes, and to the tribes, genera and species of Gramineae, including some of the more frequent aliens, by C. E. Hubbard. The ecological specialization of several of these critical plants is brought out by their distribution in Gloucestershire. For example, *Carex tumidicarpa* Anderss. is widely distributed on neutral and acid soils in the lowlands and Forest of Dean, while *C. lepidocarpa* Tausch. is

confined to wet alkaline habitats in the Cotswolds. On the other hand *C. filiformis* L. (*C. tomentosa* auctt.) presents a curious problem by its apparent indifference to edaphic conditions within its range, although it is practically confined to the Central Cotswolds in this country.

The addenda include the diagnosis of *Epipactis cleistogama* C. Thomas n.sp., which is illustrated by three of the forty-three good photographs, which give representative views of the countryside and portraits of interesting species. A Gazetteer listing parishes and place-names gives also National Grid One-Inch Ordnance Map References (as used elsewhere in the book), a procedure which might well be more generally followed. A bibliography of literature on the botany of the district, running to twelve pages, and indices complete a well-designed book.

The editing has on the whole been very careful, but local pride cannot fairly claim that 'Gloucestershire is situated between latitudes 51° 25' N. and 25° 10' N.' (p. xxvii) and the reference to *Lycium barbatum* (sic) may puzzle, especially as the plant is correctly named *L. chinense* Mill. on p. 349. But these trifling criticisms are not intended to detract from an appreciation of a useful and praiseworthy *Flora*.

D. E. COOMBE

Karl Bertsch. *Früchte und Samen. Ein Bestimmungsbuch zur Pflanzenkunde der vor-geschichtlichen Zeit.* Band 1. Handbücher der praktischen Vorgeschichtsforschung. Herausgegeben von Hans Reinert. 8·8×5·8 in. Pp. 247 with 71 pp. of figures. Stuttgart: Ferdinand Enke. 1941.

This is the first of a series of handbooks concerned with practical aspects of prehistoric investigations. It is intended to facilitate the identification of sub-fossil fruits and seeds, such as are encountered in peats, muds, etc., of glacial and post-glacial age, or such as may occur in association with prehistoric culture sites. It consists of a preface to the series, an introduction to the volume, 104 pages of keys to genera and species, and 71 pages of illustrations comprising drawings of some 1258 species. The species concerned are Central European but the majority are also indigenous in Britain.

The major grouping of fruits and seeds into rough size categories, into those with wings, those which are spherical, etc., is helpful for a preliminary narrowing down in the identification of an unknown fruit or seed.

The large number of drawings is perhaps the best feature of the book, although the standard of the drawings varies. Some, e.g. Caryophyllaceae and Labiatae, are good; others, e.g. Stratiotes, are poor and give little idea of the characteristics of the fruit or seed in question. The drawings do not always bring out the diagnostic features, for example the characteristic surface pattern of *Caltha palustris* is inadequately illustrated.

In view of the fragmentary nature of much fossil material a full artificial key is not entirely satisfactory, for identification can often be made only by the combined use of several characters. The key gives the impression (perhaps unintentionally) that a seed or fruit can be referred with certainty to its species, whereas this is not always the case. In the genus *Geum*, for example, the two species are distinguished one from the other by a size difference in the key. If, however, a fair number of specimens from each species are measured it is found that there is a considerable size range which overlaps.

Several of the drawings appear to be reproductions of published illustrations of fossil material. This technique has evident advantages since plant material in the fossil state may differ rather substantially from unprepared fresh material.

The text has a few misprints. On p. 176 for example, *Chrysanthemum alternifolium* should read *Chrysosplenium alternifolium*. On p. 124 the drawing of *Sparganium minimum* does not appear in fact to be of this species.

The chief value of the book would seem to lie in the many drawings, the major groupings in the first part of the key, some of the generic and specific characters given in the full key, all of which serve to give ideas when one is confronted with an unknown fruit or seed. These features would be more readily usable with the addition of an index to the book.

In conclusion it should be remembered that as Bertsch points out in the introduction, the final test is that the fossil and recent specimens of the supposedly similar species should correspond satisfactorily. Only then can the identification be considered correct.

J. ALLISON

Bakker, E. M. van Zinderen. *De West-Nederlandsche Veenplassen, Biologisch-Natuurhistorisch.* Pp. 136 with numerous maps, photographs and drawings. Heemschutbibliotheek. Amsterdam: Albert de Lange. 1947. Price f. 7.90.

The subtitle, *A Geological, Historical and Biological Description of the Water and Marsh Landscape*, is a fair description of this book about the Broad of the western Netherlands.

The first chapter is a geological and historical description of the country in fifteen pages, the first half telling the approved geological story, while the second half traces its history from the tenth century. Long before this, however, West Friesland was already inhabited and surrounded by many dykes, and another interesting piece of information is that turf-cutting for peat was the origin of many of the Broad, particularly in South Holland.

The second chapter, on the biology of the Broad, discusses briefly the most common successions of plant communities, and contains information about the water supply and its chlorine content. The fen district in the west Netherlands was originally a purely freshwater area, which later became brackish in the north. Underground salt-water is still a threat to successful cultivation, and in some low-lying polders it is continuously rising, to such an extent, indeed, that in the Rhineland polder about $2\frac{1}{2}$ tons of chlorine per acre are brought to the surface annually.

In the following three chapters, the reader is conducted on a tour of the individual Broad, which must be a delight to those who know them. Many historical facts are woven unobtrusively into the tapestry, and readers are struck by the author's powers of quick and clear observation and comparison. He closes with a plea for protection for these districts.

The book is well produced and enriched by artistic sketches of vegetation by J. Briede, and excellent bird photographs by N. Binsbergen; but it is expensive. Eminently readable, it is a popular field biology of the better sort, packed with interesting information, but containing no description of the various plant societies of the individual districts. Scientific names are practically not used, but there is a glossary of popular and scientific names, unfortunately only of plants. There is a classified list of literature, but no reference to sources of particular information, and no index.

C. BARCLAY

Turrill, W. B. *British Plant Life*, No. 10. *The New Naturalist*. Pp. 315, 53 colour photographs, 27 monochrome photographs, 8 maps and 2 diagrams. Collins. 1948. 21s. net.

Who is the *New Naturalist*, by whom, or for whom, this series of books has been written? It is evident that in some instances professional writers or teachers who are the *New Naturalist* seek to interest the general public in their point of view, whilst in other cases the book is directed to a public which already is composed of 'new naturalists'. In either case, the answer is the same: the new naturalist is essentially an ecologist. He is the old naturalist infected and informed by the new scientific disciplines of modern taxonomy, cytology and genetics, physiology, statistics, and the results of a very wide range of modern investigation in fields such as meteorology, soil science, archaeology, and hydrobiology.

Dr Turrill has an excellent claim to the title of the *New Naturalist* himself, for he has been for 30 years in the very forefront of the endeavour to transform the old plant taxonomy into a new experimental science. With Mr Marsden-Jones he conducted the pioneer transplant experiments of the B.E.S. at Potterne, and he has played a very notable part in establishing the new Systematics Association. Above everything else it is this kind of work which he explains and popularizes in his new book. The section of the book which deals with variation and adaptation and heredity in general terms, also includes a comprehensive account of what is known of the genetics of wild British plants. The author and publishers are well aware of the heavy demand this section must make upon the non-professional botanist, but they are undoubtedly right in regarding the interest of the matter as justifying the attempt to popularize it. It is the author's clear intention to excite the active co-operation of field botanists of all ranks in work within this field.

We may regard chapters 10-14 as dealing essentially with this theme. The content of the preceding part of the book can be seen by the first nine chapter headings, 'Introduction to the Study of British Plants', 'The Very Beginning', 'The Rise of Land Plants', 'The Ice Age and its Influence on the British Flora',

'Post-glacial Floristic Changes', 'The Present Composition of the British Flora', 'The Geographical Relationships of our Flora', 'The Habitat Factors of British Plants', 'Plant Communities, their development and modifications'. This is an exposition of the phytogeography and ecology of British plants approached from the widest possible angle. It contains a wealth of interesting botanical fact, but clearly suffers from the attempt to cover so wide a field in so short a space. Dr Turrill has given admirably the exposition of a 'New Naturalist' who is essentially a progressive taxonomist: there remains ample opportunity still for a volume from one who writes from the central position of an avowed plant ecologist and who will utilize the wealth of material now appearing in the Biological Flora and present it in this deservedly successful series.

Like all the books in the series *British Plant Life* is abundantly illustrated, and gets great charm from the colour photographs most of which are intimate portraits of plants comfortably seated at home with their associates. What a pity it is that in so many of them still the green pigmentation is inadequate. The strong etiolated yellow cast upon the leaves of *Buxus*, *Daphne laureola*, and *Vaccinium vitis idaea*, simply will not do. Great as is the advance upon monochrome, big distances remain to cover. H. GODWIN

Dillon Weston, W. A. R. and Taylor, R. E. *The Plant in Health and Disease*. Pp. 173, plates 60 and figures 6. London: Crosby Lockwood and Son, Ltd. 1948. 21s.

The heavy loss of crops caused by disease, recorded from the earliest times and still a problem of great urgency, forms the background to this book. In the early part, ancient and modern views of the nature of such disease are given. The mineral requirements of green plants are briefly stated and emphasis is laid on the importance of environment to the growth and health of crops. The structure and methods of reproduction of fungi are outlined and some interesting facts about spore-dispersal are given.

The remainder of the book is mainly concerned with crop diseases found in Britain. An account is given of seed-borne fungi and modern methods of seed treatment are described. A consideration of soil-inhabiting pathogens introduces the problem of soil 'sickness', and the necessity for sound rotations is stressed. Wind-dispersal of spores is an important factor in the spread of other fungi causing plant diseases, such as the rusts. Nutritional disorders and virus diseases are briefly reviewed. Throughout the account, the characteristic symptoms of disease and the conditions generally associated with severe outbreaks are described, and notes of resistant varieties are given. Occasional reference is made to conditions in other parts of the world where, for the same disease (e.g. Black rust), different methods of control have to be adopted. The authors' considerable experience of agricultural advisory work is clearly reflected in this account. Many of the diseases are illustrated by excellent photographs: they show diseased plants with characteristic symptoms and sometimes also affected crops in the field. A number of photomicrographs show diseased tissues and the causal fungi; most of these are good, but a few lack adequate definition.

In the concluding chapters, an account is given of the legislation designed to restrict crop diseases in Britain and the organization of the advisory services is described. Lastly, there is a classified list of diseases, chiefly of crop plants, and a number of references. This work will be valuable to pathologists and to those concerned with crop production. Ecologists may well be interested by those instances where environmental factors such as soil reaction (e.g. Club root) or weather (e.g. Potato blight) markedly affect the severity of outbreaks. J. RISHBETH

The New Naturalist, a Journal of British Natural History. Edited by JAMES FISHER with the assistance of ELIZABETH ULLMANN. Pp. 216, 12 plates in colour, 175 illustrations in black and white. 10 × 7 $\frac{3}{4}$ in. 1948. Collins. 21s. net.

The first volume of this journal consists of four parts bound together, though it is intended as soon as conditions permit to issue one part each quarter and to embody certain regular features of particular interest to amateur naturalists. The present volume contains much of value to both amateur and professional, though it is likely that the latter will appreciate particularly the contributions dealing with subjects in which he is not an expert. That is to say that the *New Naturalist* achieves its purpose and appeals to the amateur by presenting him with accurate well-written articles with an abundance of illustrations.

Each of the four parts is devoted to a particular subject, the topical features such as reviews of books, radio and films being represented, as the Editor says, 'in token form', since with the present delays in printing they could not be made sufficiently up-to-date.

The first part is concerned with Woodlands and after a brief statistical summary of the main types of woodland management continues with an account of their Post-Glacial history by Dr H. Godwin. Prof. Tansley gives a wonderfully concise description of the chief types found in the British Isles to-day and points out the modifications in their composition effected by man. Of particular interest to the plant ecologist are the articles on various aspects of the fauna, such as grey squirrels, butterflies, bird communities, and the excellent account of the tits, all of them subjects of which he is ordinarily very ignorant. Stephen Potter contributes a lively article on books and the amateur naturalist.

The remaining parts follow the same general plan but with other topics—The Western Isles of Scotland, Migration and The Local Naturalist—with articles by such well-known writers as Fraser Darling, C. B. Williams, Peter Scott, R. M. Lockley, J. S. L. Gilmour and W. H. Pearsall, to mention only a few.

In a journal which is so obviously authoritative and accurate it is perhaps a little unfortunate that no indication is given of the debatable nature of the conclusions which have been drawn from recent discoveries on the Isle of Rhum, particularly in view of the possibility that some of the remarkable plants found there have been introduced.

The format is in the pleasing style that we have come to associate with the *New Naturalist* series of books and the type admirably clear. It is regrettable that the volume is not altogether free from blemishes. The review copy had two pages loose and another one spoilt by some curious mishap in printing; another copy picked up at random in a book-shop had four blank pages in the middle of an article. In spite of these chance imperfections, which it is to be hoped can be avoided in future issues, the journal well merits the attention and support of all interested in any aspect of natural history.

T. G. TUTIN

Good, Ronald. *A Geographical Handbook of the Dorset Flora.* Pp. xii + 256, with frontispiece and 42 maps. Published by the Dorset Nat. Hist. and Arch. Soc., and obtainable from the Curator and Secretary, County Museum, Dorchester. 1948. Price 20s.

Phytogeography and Ecology are terms which at one time were thought to be more or less synonymous, but which have now come to stand for somewhat distinct methods of study of the distribution phenomena of plants in nature. Prof. Good, whose recent book on 'The Geography of the Flowering Plants' was recently reviewed in this journal, is a plant geographer whose latest work illustrates how closely the two methods may approach without losing their recognizable identity. Roughly speaking we might say that the plant geographer is interested in the areal distributions of species for their own sakes, and that he seeks to establish general principles through comparison and analysis of the types of distribution areas. By contrast the ecologist (though not indifferent to those issues) seeks rather to establish by field and laboratory observation and experiment the causal mechanisms which are responsible (amongst other things) for the distributional relationships.

Most phytogeographers have been concerned with distribution over relatively large areas, as for instance by vice-counties across a country, but here the author has undertaken a scale of investigation intermediate between this and the very small scales generally employed by ecologists, scales in metres or decimetres often enough. Prof. Good has undertaken investigation of his home county, Dorset, by the process of listing a very large number of **stands** distributed as evenly as possible over it. Each locus was in a 'well-defined and circumscribed plant habitat, such as a bog, a pasture-field, or a small wood' or else 'was a representative portion of a more extensive area such as a chalk down or a hedgerow'. There were over 7500 such stands, all accumulated by the one observer, at an average density of 7 or 8 per square mile (3 per sq.km.).

The data thus obtained have been plotted in dot distribution maps for the whole area of the county, and by inspection the distribution figure for every Dorset species can be correlated with the distribution of those factors likely to be concerned in determining it. The county is about 48 miles by 40 (78 km. by 65), and lies on the south coast of Britain, is rich in species of southern distribution, presents a very complex and interesting range of rock and soil types, has a moderate altitudinal range, and rather con-

siderable rainfall differences: altogether an admirable region in which to explore distribution data at the chosen scale.

The book naturally falls into two parts. The one is a detailed handbook, giving the distributional data for all the flowering plants of Dorset, a list which will be of the greatest value to all ecologists, and to naturalists interested in many groups of organisms besides the flowering plants, and a record of permanent value. The other part of the work is the analysis of the mass of data acquired in the survey, and it is here that the wide general interest of the book is to be found. This part is illustrated by 42 maps, 12 of them illustrating the distribution of such values and conditions as rainfall, drainage, and soil-types, whilst the rest are species maps.

A full description of the soils is given in a separate chapter contributed by Mr K. L. Robinson, and it is a most valuable feature. Chapters 4-8 deal with the history and constitution of the Dorset flora, with the distribution inside the county of various categories of plants, and with the influence of various factors upon distribution. No British botanist can fail to find here data of interest about the behaviour in this region of species familiar to him elsewhere, but the importance of the work goes far beyond this, lying chiefly in the proposed interpretations of distributions upon the basis of the Dorset correlations. The analysis has brought to light endless features of interest, and innumerable problems for further study: many explanations are put forward speculatively, and the need is evident for testing them by experiment and further observation. This might apply for instance to the species thought to be controlled by the rainfall, such as *Primula vulgaris*, *Phyllitis scolopendrium*, and *Polypodium vulgare*, all of which increase westwards; to the species thought to require high temperatures, such as *Erica ciliaris*, *Cicendia filiformis*, *Asparagus maritimus*, and others for which the county is famous; and to *Juniperus communis*, *Filipendula hexapetala* and *Verbascum nigrum* which are more abundant in the north than in the south of the county: indeed the possibilities are legion.

The author writes with acceptable candour and does not cloak his meaning: you may disagree but at least you know what he means when he writes: 'The key to a proper appreciation of the Dorset flora and its constitution is the realization that it is very largely an immigrant flora which has gradually colonized the county from without, and that the addition of fresh species to it, by this process, has been going on, probably without cessation, for many thousands of years.' As appears elsewhere in this journal, the reviewer is inclined to think that the invasion processes may have been more discontinuous than is here allowed, and likewise that many species ranked by Good as recently established adventives were in reality widespread in Britain in Late-Glacial times. One casts glances towards the many ancient peat deposits of the county and of neighbouring Hampshire, wherein there probably lie those sub-fossil plants which would settle these questions of status.

The arrangement of material and the format are attractive, but a possible improvement would be to make the index refer not merely to the hand-list, but also to the general and descriptive section of the book, where so many interesting comments are embedded. This would facilitate use of the book by such folk as the authors of accounts for the Biological Flora: not only will they find much of value herein, but may, I feel sure, call also upon Prof. Good's primary data and his wide field experience.

H. GODWIN

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6-7 JANUARY 1949

Thursday, 6 January

The winter meeting of the Society opened at 8 p.m. on Thursday, 6 January, with a Soirée in University College, about 100 members and guests being present. Refreshments were served in the Women's Staff Common Room, and many interesting ecological exhibits were displayed in the Professors' Smoking Room and in the Department of Architecture. Prof. Pearsall and Dr F. W. Jane showed photographs, water-colours and maps of mountain habitats and of Blakeney Point, and a strikingly informative aerial photograph of Esthwaite Tarn. Dr Jane also showed his beautiful photomicrographs of various woods. Mr B. A. Jay's close-up photographs of coniferous shoots demonstrated the value of really good photographs for showing morphological details, and Mr R. Brinsden's Dufay colour transparencies reproduced autumn colorations with great faithfulness. Mr P. Bell's exhibit consisted of photographs of Swiss conifers and herbarium sheets of *Carices* collected on and near the Albula Pass (2316 m.) in the Rhaetic Alps. The sedges included several which occur, often as very rare plants, in the British flora (*C. microglochin*, *rupestris*, *atrata*, *humilis*, *paupercula*, *ericetorum*, *montana*, *ornithopoda*), as well as species not found in this country. Miss E. Archibald demonstrated her multiple-quadrat method for studying the structure of plant communities, and Miss Stella Champness showed the results of her analyses of grasslands by methods which give information about changing composition during the establishment of long-term leys. There were also four exhibits involving algae. Dr Fogg and E. F. Wilkinson showed some exquisite water-colour studies of the blue-green algae *Anabaena cylindrica*, *Petalonema alatum*, *Gloeocapsa* spp. and *Scytonema* sp.; Dr G. Abdin demonstrated the diatom flora of a Blakeney salt-marsh; M. R. Suxena illustrated his work on the algal flora of Hyderabad, and C. B. Rao his studies of algal periodicity in small ponds. Rocky lakes at 1200-2000 ft. in eastern Hyderabad have a plankton flora in which species of *Euglena*, *Phacus*, *Trachelomonas*, Diatoms, Desmids and Chlorococcales are prominent; dripping rocks are characterized by *Cosmarium botrys* var. *laeve* and *Fischerella* sp., and rice fields at low levels by the blue-green *Johannibaptistia pellucida*. In small ponds in south England C. B. Rao has attempted to correlate peaks in the abundance of various plankton constituents with climatic factors and with changes in the chemical constitution of the water. Peaks in Euglenophyceae have coincided with low concentrations of albuminoid ammonia in spring and summer, peaks in Diatoms have followed periods of high silica, nitrate and phosphate content in spring and early autumn, and Chlorococcales and Desmids have been abundant when water temperature and hours of sunshine have been high.

Prof. Pearsall, Dr and Mrs Jane and other members of the staff of the Department of Botany and the Governing Body of University College are much to be thanked for a most pleasant evening, one of many enjoyed by the Society in University College.

Friday, 7 January

At 11 a.m. on Friday, 7 January, the Annual General Meeting of the Society opened with the reading and signing of the minutes of last year's annual meeting and with the reading of apologies for absence.

The report of the Honorary Secretaries upon the work of the Society in 1948 was read and accepted in the form already approved by the Council:

Report of the Hon. Secretaries for the year 1948

The thirty-fourth Annual Meeting of the Society, attended by more than 80 members and guests, was held in the Departments of Botany and Zoology of Bristol University on Friday, 9 January 1948, following a Soirée and an exhibit of ecological work on the previous afternoon and evening. The business meeting

at 10 a.m. was followed by three papers on the hydrography and ecology of the Lough Ine Rapids, and after lunch by three further papers on plant ecology. The Society is most grateful to Prof. Macgregor Skene and J. E. Harris and their colleagues for organizing a very pleasant and instructive meeting, and to the University authorities for providing accommodation.

On Wednesday, 28 April 1948, in the Botany Department, University College, London, a joint meeting was held with the British Society of Soil Science, the subject for discussion being 'The Organic Matter of the Soil'. The meeting, which was very well attended, lasted from 10.30 a.m. until 5 p.m. and aroused very considerable interest. Mr C. G. T. Morison, President of the British Society of Soil Science, was in the Chair, and six papers were read, three by members of each Society. It was of peculiar value as showing the extent of the gap which remains between the approaches to the subject by the soil scientists and the ecologists.

The Summer Meeting was held at Newcastle-upon-Tyne from Monday, 5 July, until Friday, 9 July, accommodation being provided at the University Halls of Residence. The meeting began with a Soirée in the Department of Botany, King's College, Newcastle, by kind permission of Prof. Meiron Thomas. On the following four days the party enjoyed a series of field excursions which included memorable visits to the Farne Islands and to Teesdale, and some relaxation from ecology in the form of a conducted tour of Durham Cathedral and a dinner in Durham Castle. Our best thanks are due to Drs G. Varley and D. Valentine and their colleagues for arranging an excellent programme, and to the University authorities and the Heads of the Biological Departments at Newcastle and Durham for their kind hospitality.

On Tuesday, 19 October 1948, there was held in the rooms of the Geological Society, Burlington House, a joint meeting with the Society for the Promotion of Nature Reserves. His Grace the Duke of Devonshire was in the Chair, and there were present about 70 members of the two Societies. Papers on the aims and principles of nature conservation were read by Prof. A. G. Tansley, Capt. C. Diver and Dr H. Godwin, and the meeting concluded with the showing of an American instructional film dealing with related topics, which was kindly loaned by the Conservation Foundation which had been responsible for making it.

During the year further progress has been made in overtaking arrears of publication of the *Journal of Ecology*. Vol. 35, belonging properly to 1947, appeared as a single issue early in the year, and the first number of Vol. 36 came out in July, so that publication is now only one half-yearly number in arrears. Vol. 35 contains 310 pages, with twelve original articles, and also reviews, notices and four parts of the Biological Flora. The first number of Vol. 36 contains 235 pages, with nine original articles, reviews, notices and two parts of the Biological Flora.

The second number of Vol. 16 of the *Journal of Animal Ecology*, which appeared in January, contained 125 pages with seven original articles, one review and notices; and the first number of Vol. 17, appearing in September, contained 100 pages with eight original articles, reviews and notices.

Since the last Annual Meeting the membership of the Society has risen from 550 to 595 members, 10 members having resigned or died, and 55 new members having been elected. Of the present membership 310 members take the *Journal of Ecology* alone, 180 the *Journal of Animal Ecology* alone, 99 members receive both *Journals*, and 6 neither.

During the year there were published in the *Journal of Ecology* accounts for the Biological Flora of the genus *Melandrium*, of *M. album*, *M. dioicum*, *Suaeda maritima*, *S. fruticosa*, the genus *Sonchus*, *S. oleraceus* and *S. asper*. We regret to have to record the death of Dr A. Smith, who from its beginning acted as our advisor upon fungal diseases of species dealt with in the Biological Flora. We are happy to report that Dr N. F. Robertson, of the Botany School, Cambridge, has agreed to undertake the same function.

The Society greatly regrets the loss of a distinguished member by the death of Dr M. C. Rayner.

We note with pleasure the election of Capt. C. Diver as the first Director-General of the newly instituted Nature Conservancy.

A. R. CLAPHAM } *Hon. Secretaries*
L. A. HARVEY }

The Hon. Treasurers' report was read by Dr A. S. Watt, Mr V. S. Summerhayes being prevented by illness from attending the meeting. Expenses during 1948 had been about average, and there had been about £100 additional income from subscriptions compared with last year. The collection of subscriptions had proceeded satisfactorily. Dr Watt concluded by proposing that Messrs Wm. Norman and Sons be

reappointed the Society's auditors and that the annual grant of £10 to the Freshwater Biological Station should be renewed in 1949, both proposals being accepted. Prof. Tutin then proposed that the Society should express its thanks to the Hon. Treasurers for their devoted work. This was seconded by Prof. Tansley and carried unanimously. Mr H. Cary Gilson expressed on behalf of the Freshwater Biological Association their thanks to the Society for the renewal of the annual grant. After agreeing to Mr Elton's proposal that a grant be made to Dr Hobby in recognition of his services to the *Journal of Animal Ecology*, the Society proceeded to the election of Officers and members of the Council as follows:

Vice-President: C. DIVER.

Hon. Secretaries: A. R. CLAPHAM, L. A. HARVEY.

Hon. Editors: H. GODWIN, C. S. ELTON.

Hon. Editors of the Biological Flora: A. R. CLAPHAM, H. GODWIN, P. W. RICHARDS.

Ordinary Council Member: W. B. TURRILL.

The President, Mr C. S. Elton, then drew the attention of the Society to the appointment, on 1 November 1948, of one of its members, Capt. Cyril Diver, as Director-General of the new Nature Conservancy, the setting up of which followed the adoption of the White Paper on Nature Conservation. The Society had contributed in important ways, through its Reports and through its representatives on various committees, to the compilation of the White Paper, and should be well satisfied that the Government had accepted the proposal that there should be a Biological Service. For various reasons the designation Nature Conservancy was preferred to Biological Service, but the field of activity of the new organization would be that contemplated in the White Paper. The Society would wish to convey to Capt. Diver its appreciation of the honour done him and to assure him of the Society's collective and individual support. Prof. Tansley said that this new venture had very great potentialities but would need the support of all sympathizers. Its efforts would lead to the preservation of areas of ecological interest, and the Society should assist to the limits of its powers.

The Society next proceeded to the election of nine new members, after which Dr Godwin reported on the position of the *Journal of Ecology*, stating that the second number of Vol. 36 should appear in a week or two and appealing for further papers for publication. Mr Elton apologized for the delay in appearance of the second number of the *Journal of Animal Ecology* for 1948, but said it was expected hourly. Prof. Clapham stated that during 1948 there appeared accounts for the Biological Flora of *Melandrium album* and *M. dioicum*, *Suaeda fruticosa* and *S. maritima*, *Sonchus oleraceus* and *S. asper*. He repeated last year's appeal for a more rapid preparation of shorter accounts so that a greater number might appear in each future volume. The Society would learn with great regret the loss by death of the valued and devoted services of Dr Alexander Smith who had from the beginning acted as mycological referee for Biological Flora accounts. It was, however, a pleasure to learn that Mr N. F. Robertson of Cambridge had agreed to take Dr Smith's place.

Mr Elton then proposed from the Chair that Rule 8 of the Society's Constitution, at present reading: 'The Society shall be governed by a Council of not less than fifteen, and not more than twenty Members consisting of the Officers of the Society, namely the President, two Vice-Presidents, the two Hon. Editors, the two Hon. Secretaries and the two Hon. Treasurers, with ordinary members of Council', should be amended by replacing the word 'twenty' by 'twenty-five'. Dr Watt seconded the proposal, explaining the desirability of increasing the scope of membership of the Council so that a wider range of related branches of science should be represented. The proposal was carried.

Mr A. J. Wilmott appealed for experiments which might throw light on the frequent origin of pure stands of single species in such habitats as railway cuttings, and suggested that soil from such places might be potted to see what seeds were already present.

Mr C. S. Elton then gave his thoughtful and stimulating Presidential Address on 'Population Inter-spersion', after which the Society adjourned for lunch in the Refectory of University College.

The afternoon session began at 2.15 p.m. with Dr V. M. Conway's paper on the 'Surface Ecology of Ringinglow Bog'. Dr Conway showed that the bog may be regarded as consisting essentially of two flush areas with a low *Calluna*-dominated watershed. The north-west flush can be seen from stratigraphical investigations to have been substantially the same throughout the latter part of its development, still

retaining the *Juncus* spp. and *Sphagna cuspidata* which always characterized it. The eastern flush, however, shows *Sphagna cymbifolia* (chiefly *S. magellanicum* and *S. papillosum*) below a few cm. of *Eriophorum vaginatum* peat, indicating a great change in surface vegetation perhaps 150 years ago. This change Dr Conway ascribed to the cutting of drains which since became ineffective. The initial effect of drainage is presumed to have been the disappearance of *Sphagna* and the increased luxuriance of *Eriophorum vaginatum*. Neglect of the drains has led to a restoration of the water-table and a decrease in the vigour of the cotton-grass, but the *Sphagna* have not yet succeeded in returning to dominance, though there appears no reason why they should not do so in the course of time. Dr A. S. Watt, Dr H. Godwin, Prof. W. H. Pearsall, Prof. A. R. Clapham, Mr A. J. Wilmott and Dr E. W. Jones took part in a discussion in which Dr Conway indicated that she was not convinced that atmospheric pollution had played any major role in initiating the changes described.

Miss E. E. A. Archibald, in her paper on 'Plant Populations', said that she had been seeking biometric standards applicable for determining the specific character of a plant community, and had restricted her investigations to natural communities which had probably not suffered recent change in dominant species. Only communities of uniform life form had been studied: chalk grassland, Nardetum, Eriophoretum and some maritime communities. The communities were delimited subjectively, and quadrats of various sizes were listed, only the presence of each species being recorded, irrespective of the number of individuals by which it was represented. Quadrats were located at random, with the restriction that one quadrat of each size was based on each location. From these data collected on twenty quadrats of sizes ranging from 1 sq.cm. to 64 sq.m. it was possible to determine the quadrat area giving on the average 50% of the total number of species present in the community. The curves obtained when average numbers of species were plotted against log quadrat area showed very close agreement with curves calculated from a theoretical relation which were S-shaped with a point of inflexion at the 50% area. In this theoretical expression the logarithm of the ratio of the average number of species for any given quadrat size to the differences between this and the total number in the community is proportional to the logarithm of the ratio of the size of the quadrat to the area carrying 50% of the total number of species. The proportionality constant appears to be the same for all the communities studied, a most interesting finding. The most important biometric features appear then to be the specific density or average number of species per unit area, and the 50% area, which measures the size of the unit pattern. When the reciprocal of the specific densities are plotted as ordinates against log 50% areas, a U-shaped curve is obtained with its minimum at a 50% area of about 1 sq.m., this forming a convenient line of separation between communities of small and those of large pattern. Mr Wilmott, Mr Rutter, Dr Spooner, Dr Godwin, Prof. Clapham and Col. Buxton took part in the discussion which followed a thought-provoking paper.

Dr O. W. Richards read the paper by himself and Miss N. Waloff on 'Some Ecological Observations on British Short-horned Grasshoppers'. The eggs of these grasshoppers are laid in pea-sized egg-pods in July to October but do not hatch before the following year. Some species (e.g. *Omocestus ventralis*, *Chorthippus parallelus*, *C. bicolor* and *Mymecotettix maculatus*) lay their eggs only in loose soil, while others (e.g. *Omocestus viridulus*, *Stenobothrus lineatus* and *Chorthippus albomarginatus*) lay in grass or amongst leaves. The egg-pods may be found by careful searching in samples of soil or turf. Species which lay in bare soil are confined to ant-hills in ordinary pasture. In the subsequent discussion Dr Uvarov stated that the overgrazing of grassland is associated with grasshopper plagues in the United States and elsewhere, and that this showed the importance of studies such as those reported by Dr Richards. Prof. Harvey and Dr Turrill also took part.

Dr A. R. Gemmell read the concluding paper on 'The Effect of Sexual Mechanisms on the Production of Varieties and the Distribution of British Mosses'. Although dioecious moss species are less fertile than monoecious species, yet they occupy a higher average number (58) of vice-counties than do monoecious species (42), species sterile in the British Isles following with an average of only 13 vice-counties. Dr Gemmell suggested as an explanation for this series that dioecious mosses, which are necessarily outbreeding, will show superior genetic versatility to monoecious types, which in their turn will be superior in this respect to sterile types. This genetic versatility will lead to physiological and ecological versatility of the species, increasing both the rate of spread and the capacity for continued spreading. Drs P. W. Richards, Spooner, Turrill, Ross and O. W. Richards and Prof. Tutin took part in an interesting discussion.

The President, Mr C. S. Elton, ended by expressing the Society's gratitude to Prof. Pearsall and his colleagues for arranging so successful and enjoyable a Meeting, and by thanking Miss Winifred Curtis for yet again providing milk and butter for the Soirée.

JOINT MEETING WITH THE SOCIETY FOR THE PROMOTION OF NATURE RESERVES

19 OCTOBER 1948

A Joint Meeting with the Society for the Promotion of Nature Reserves was held in the rooms of the Geological Society in Burlington House on the afternoon of 19 October 1948. His Grace the Duke of Devonshire was in the Chair, and there were present about seventy members of the two Societies. The Chairman opened by welcoming this first joint meeting of societies with many common interests, both engaged in working for the preservation of our heritage of natural beauty in the face of the many dangers which threatened it at the present time. He hoped there would be many such gatherings in the future.

The first paper was read by Prof. A. G. Tansley, F.R.S., who emphasized the two main aims of nature conservation: to preserve the character and beauty of our countryside, and to preserve for scientific investigation adequate samples of that countryside. The two aims were often merged in the minds of scientific investigators, and this tended to obscure their fundamental distinctness, but the ways of achieving them might be different and they must be separately considered. Not all people wanted these things, and there was need for an education of public opinion. The first aim had a widespread appeal. Foremost in promoting it had been the National Trust and the Council for the Preservation of Rural England, but of late it had become increasingly evident that more was needed and that public authority must take a hand. In 1947 the National Parks Committee recommended that certain large areas of wild and beautiful country, necessarily including some villages and small towns, should be treated as National Parks. This did not mean that they should no longer be used for agriculture. It was an essential part of the idea that such pursuits should continue, but that radical changes in character should be regulated with great care, while facilities for public enjoyment should be maintained and increased. In the coming session of Parliament a new Bill would embody these recommendations. There had been controversy about the constitution of the bodies to be charged with implementing the proposals. County Councils complained that a central body would control development in areas cutting across existing county boundaries, and so would cause serious friction. But the administration of a single National Park by several County Councils seemed no less likely to cause trouble, and it was to be hoped that a satisfactory solution would soon be found.

The National Parks Committee also recommended the recognition of a number of Conservation Areas, within which any exploitation or development must be agreed by all interested parties, including those whose primary interest was in nature conservation. Opponents of the scheme argued that such regulation would sterilize development in large tracts of country. There was, however, no intention to regulate closely, but only to safeguard amenity and scientific interests.

The second aim of nature conservation, the preservation of samples for scientific study, implied the setting apart of relatively small areas as Nature Reserves. Many such reserves already existed, thanks to the devoted activities of certain local natural history societies and to the valuable work of the Society for the Promotion of Nature Reserves. It had been recognized that these reserves also must be managed by some public or local authority with the necessary powers, and the Wild Life Conservation Special Committee set up by the Ministry of Town and Country Planning to advise on this matter had recommended the formation of a Biological Service to manage and control the National Nature Reserves, over seventy in number, for which it asked. The new Service should not merely be responsible for managing the Reserves but should consider problems relating to wild life in the country as a whole, should carry out and provide facilities for continuous scientific investigation, act as a clearing house for available information, and give advice on practical problems such as those that would arise in managing the National Parks. This important recommendation had been accepted by the Government, and a first Director had been appointed, though his name had not yet been officially announced. It was essential that the work of the Service should be efficient and should command confidence, and it was hoped that suitably qualified people would come forward.

Captain C. Diver regretted that he had been unable to revisit Studland Heath since 1939. It had been used by the Fighting Services for experimental work during the War, but the operations involved in making it safe again for civilian use had been more destructive than the original damage. Air-photographs had been supplied by the Navy in 1936, but no further surveys had been possible and time had been lost in studying the recovery process. Many new habitats, especially aquatic habitats, had been formed, and these ought to be mapped regularly by air photography. It was most important to study changes arising from interference, for this would supply the kind of knowledge upon which management for conservation must be based.

It might be said in general terms that the fundamental question to be answered was 'What kinds of plant and animal live how and when and where and why?' The task might be tackled partly by direct observation and partly by the application of experimental and mathematical techniques. The role of direct observation must not be underestimated; sorting out the facts about any community made the highest demands on intelligence. It was essential first to collect background information about the physiography, geology and past history of the area. Old maps, records and drawings might be very valuable but must be used critically. Next came the analysis of the plant cover by recognizing and listing the various plant communities. This gave only the framework, however, for the more detailed study of the distribution of plant populations which would be needed; a single wood 2 acres in area had proved to be a mosaic of 280 recognizably different subhabitats in the field layer alone. After this it would be necessary to understand the breeding structure of the communities. How few individuals, and how sparsely spaced could constitute a breeding unit? How much active and passive migration took place, and how far did this establish new populations or modify old ones? This kind of detailed information was pertinent to Nature Conservation, which must be based on an intimate knowledge of natural populations.

Dr H. Godwin, F.R.S., opened by saying that it fell to him to show how principles referred to by the two previous speakers applied unmistakably in a particular instance. He dealt briefly with the history of the East Anglian Fenland, illustrating his talk with lantern slides which showed the replacement of old river-courses by new cuts, especially in Romano-British and modern times; and the increasingly elaborate machines, from windmills to diesel engines, required to pump water from peat whose surface level was steadily falling as the result of drainage. It was no easy matter to maintain the high water-table in Wicken Fen when all the surrounding land had been drained, but the difficulties had been overcome. There were, however, other and no less important problems of management of the Fen as a Nature Reserve. The vegetation was a mosaic of plant communities whose interrelations had not at first been readily intelligible. There was a close dependence upon the height of the water-table, quite small changes in which were associated with striking vegetational changes. Dr Godwin recalled that Dr Gabrielson, of the United States Wild Life Conservation Board, found that vast changes had been found in reserves in the U.S.A. following alterations of only 10 cm. in water-table. Amongst the consequences of a lowered water-table was invasion by woody plants which soon shaded out the more light-demanding fen plants, including the very local *Peucedanum palustre* upon which the caterpillars of the Swallow-tail Butterfly feed. This was a natural successional sequence and it was clear that conservation of the special fen flora and fauna demanded active measures of control. Other vegetational differences were found to be independent of water-table and had been shown to be the result of different modes of exploitation of the fen communities for litter and thatching materials in the past. Only by the continuation of the appropriate kind and degree of human interference could these communities be maintained, a point of great importance in any consideration of principles of management of nature reserves.

The meeting closed with the showing of an American instructional film, the first four reels of a series to be entitled 'The Living Earth'. The Hon. Miriam Rothschild, who had secured the film, gave a preliminary talk in which she explained that it was intended as propaganda for nature conservation, that it was aimed primarily at schoolchildren, that the set of four reels cost 900 dollars, and that it was paying its way in the U.S.A. The first reel, 'Top Soil', stressed the significance for plants of the upper layers of the soil; the second, 'The Vital Earth', dealt with the concept of balanced communities consisting of animals as well as plants, and showed how deficiencies in a single trace element might upset this delicate balance and lead to infra-optimal growth of many or all of the constituent organisms; next, 'Arteries of Life' described the water economy of a balanced community under natural conditions, picturing the role

of forests, rivers, marshes, beavers and other constituents of the complex system involved; finally, 'Seeds of Destruction' showed the insidious or catastrophic consequences of an unheeding disturbance of the balance of the ecosystem, resulting in soil erosion by water and wind, floods and droughts, crop failure and famine. The photography was excellent and the schematic representation clear and emphatic, while the commentary struck about the right note for combining interest with instruction. It was agreed that a similar venture should be made in this country, and appreciation was expressed of the offer of help made by Mr George F. Brewer of The Conservation Foundation of the U.S.A., which with the New York Zoological Society was responsible for producing the film.

In conclusion the Chairman thanked the speakers and the Hon. Miriam Rothschild for their contribution to an interesting and successful meeting.

BIOLOGICAL FLORA OF THE BRITISH ISLES

L.C. (Ed. 11) Nos. 1987-1991, 1993

ELEOCHARIS R.Br.

S. M. WALTERS

The limits of the genus *Eleocharis* are taken, as in Svenson's monograph (1929, 1939), to include in Britain the species *E. pauciflora* (Lightf.) Link (*Scirpus pauciflorus* Lightf.) and *E. parvula* (R. & S.) B., N. & S. (*Scirpus nanus* Spreng. etc.), in addition to the four species normally referred to this genus in British Floras. The genus may be defined as a group of plants allied to *Scirpus*, but differing in the possession of a single terminal ebracteate spike on a haulm bearing leafless sheaths, and a fruit with a distinctly differentiated and often swollen style-base. It is in respect of the fruit character that *Eleocharis pauciflora* and *E. parvula* are somewhat aberrant. Thus defined, the genus contains six British species, arranged according to Svenson as follows:

Series Pauciflorae:

E. parvula (R. & S.) B., N. & S., *E. pauciflora* (Lightf.) Link.

Series Aciculares:

E. acicularis (L.) R. & S.

Series Multicaules:

E. multicaulis Sm.

Series Palustriformes, subseries Palustres:

E. palustris (L.) R.Br. em. R. & S., *E. uniglumis* (Link) Schult.

These two species are very closely related, but are normally satisfactorily separable on a few morphological characters. Plants exhibiting some intermediate characters occur, particularly in coastal habitats of the west and north of Britain; their status is as yet uncertain, and requires further investigation.

Cytology. A number of different chromosome numbers occur in those species of the genus which have been investigated. There is evidence for basic numbers of $x=5$ and 8, but in the Palustres in particular several different and not obviously related numbers have been found. The basic number $x=5$ is shown in *E. multicaulis* with $2n=20$ (Håkansson, 1928), *E. parvula* with $2n=10$, *E. acicularis* with $2n=20$ and '*E. palustris*' (Russian material) with $2n=10$ (Darlington & Janaki-Ammal, 1945). A diploid chromosome number of 16 has been recorded for '*E. palustris*' from Russia, North America, Scandinavia (Darlington & Janaki-Ammal, 1945) and with British material of *E. palustris* (cf. separate account); higher numbers from $2n=36$ to c. 46 occur also in the Palustres, the widespread north European *E. palustris* having typically $2n=38$, and *E. uniglumis* typically $2n=46$.

Evidence of cytological irregularity was found by Hicks (1929) in both '*E. palustris*' and *E. acicularis*; similar evidence of varying metaphase bivalent numbers in the same individual has been recently found in British *E. uniglumis* material, and Doxey (1938) recorded diploid numbers from $2n=37$ to 40-41 in northern English *E. palustris*. There is

obviously a complex cytological situation in the *Palustres* parallel to the taxonomic complexity (cf. separate accounts).

Habit and life-form. The six British species are all herbaceous perennials, but differ considerably in some cases in habit and mode of perennation. In the *Palustres* the adult plant consists of an underground rhizome system bearing erect leafless photosynthetic haulms, some of which terminate in the simple spike. 'Primary' haulms originate singly at each node of a young rhizome, and others are produced in tufts from a bud at the base of each of these 'primaries'. The degree of development of the rhizomatous or the caespitose habit varies greatly (see separate account). Essentially the same type of growth is found in *E. acicularis*, although the plant is very much more slender, and may occur in an entirely submerged form. In *E. multicaulis*, no long rhizome is produced, and the caespitose plant is morphologically equivalent to a tuft of *E. palustris*. Finally, the *Pauciflorae* differ in having very slender rhizomes bearing one or two scale leaves and terminating either in a new tufted daughter plant or, in autumn, in a specialized perennating bud. In *E. pauciflora* itself, both the parent tufts and the offsets normally survive the winter, whereas in *E. parvula* only the offsets survive. *E. parvula* has often inaccurately been described as an annual because of this mode of perennation.

Flowers. The flowers in all species are borne singly in the axils of the spirally arranged glumes in the simple terminal spike. They are inconspicuous, markedly protogynous, opening in strict succession up the spike, and normally wind-pollinated. There is no evidence of apomixis, and fruit is set freely in all the species. The leafless haulms may be purely vegetative, or may bear the terminal spike; but in the *Palustres* at least it is clear that all haulms are potentially spike-bearing, as a spike rudiment can be seen at the tip of the vegetative ones.

Ecology. The six species are all restricted to damp habitats where competition from tall-growing species is slight or absent. (*E. acicularis* may occur as a completely submerged aquatic.) The detailed description of the habitats is given in the separate accounts, but a general comparison between the four species, *E. palustris*, *E. uniglumis*, *E. pauciflora* and *E. multicaulis*, would be useful here, as they are superficially similar, and often confused in the field. These four species differ considerably in their soil preferences. *E. palustris*, the most widespread, is, as would be expected, most tolerant, and may occur in habitats with alkaline, neutral or slightly acid soil water. *E. uniglumis* seems to be confined to soils with a neutral or alkaline water supply, and is particularly characteristic of brackish marshes near the sea, but is by no means restricted to coastal habitats. *E. pauciflora* occurs on alkaline marshes and fens where competition is slight, whilst *E. multicaulis* is restricted to acid soils, such as damp sandy heaths, and bogs. Thus *E. palustris* may be found growing with any of the other three species (although it is not common on acid soils); *E. pauciflora* and *E. uniglumis* may grow together in inland habitats; whilst *E. multicaulis* will only be found growing in close proximity to *E. pauciflora* where there is considerable local variation in soil acidity.

The differential effect of soil-water acidity is very well seen in the zonation at Derby Fen, near King's Lynn, Norfolk; here a typical fen vegetation is developed in an area subject to flooding by the Gaywood River, the waters of which are base-rich. Immediately above the zone of influence of the calcareous water, however, an acid-heath vegetation is developed on the sandy soil. The zonation at a particular point on the margin may be described as follows:

(1) Innermost zone, with tall-growing fen species, *Juncus subnodulosus* and *J. articulatus* subdominant; no *Eleocharis*.

(2) Marginal zone, with shorter species; *E. uniglumis* and *E. pauciflora* abundant (cf. Table 1, no. 6, in account of *E. palustris*).

(3) Wet acid-heath zone above summer water-level; *E. multicaulis* and *Scirpus setaceus* abundant, with *Anagallis tenella*, *Drosera rotundifolia*, etc.

In this zonation, the boundary between (2) and (3) is remarkably clear.

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Eleocharis palustris (L.) R.Br. em. R. & S.

S. M. WALTERS

Perennial herb, with long underground rhizome and erect leafless haulms; very variable in size and habit, from small rather caespitose plants only a few cm. in height, to loose strongly rhizomatous plants with thick haulms up to 1 m. tall. Spikes borne terminally, many-flowered (25-70), with two subequal sterile basal glumes, one slightly overlapping the other, but rarely more than three-quarters surrounding spike at base. Fruit biconvex with style-base often longer than broad; bristles 4, usually (in British material) exceeding fruit; fruit surface faintly punctate-striate under lens.

Two subspecies exist in Britain;* they may be distinguished as follows: subsp. *vulgaris* Walters. Ripe fruit (1.3) 1.45-1.8 (2.0) mm. long, excluding style-base; middle glumes of spike 3.5-4.5 mm. long; glumes rather variable in colour, but usually brownish; stomatal length (on epidermis from middle of haulm) 0.065-0.085 mm. Chromosome number $2n = 38$.

subsp. *microcarpa* Walters. Ripe fruit (1.1) 1.2-1.4 (1.5) mm. long, excluding style-base; middle glumes of spike 2.75-3.5 mm. long; glumes rather pale often light brown or straw-coloured, usually more easily detached from ripe spike than in subsp. *vulgaris*. Stomatal length (on epidermis from middle of haulm) 0.05-0.065 mm. Chromosome number $2n = 16$.

E. palustris (L.) R.Br. em. R. & S.

subsp. *vulgaris* subsp. nov.

Spicae saepissime 20-40 florum; squamis mediis 3.5-4.5 mm. longis, fuscis; achenio (stylopodio excluso) (1.3) 1.45-1.8 (2.0) mm. longo; stomata (in epiderme medii culmi) 0.065-0.085 mm. longa. Chromosomata $2n = 38$.

Typus: in pratis humidis, Hauxton, Cambs. 21. vii. 46; in Herb. Univ. Cantab.

subsp. *microcarpa* subsp. nov.

Spicae saepissime 40-70 florum; squamis mediis 2.75-3.5 mm. longis, pallidi-fuscis, saepe caducis; achenio (stylopodio excluso) (1.1) 1.2-1.4 (1.5) mm. longo; stomata (in epiderme medii culmi) 0.05-0.065 mm. longa. Chromosomata $2n = 16$.

Typus: in fossa in pratis humidis, Graveney Marshes, near Whitstable, east Kent, 16. ix. 46; in Herb. Univ. Cantab.

Certain varietal names of continental authors have been applied to British material. The following include those most commonly used:

var. major auct. Most plants so called are vigorous aquatic forms of subsp. *vulgaris*, but the plasticity of both subspecies is such that large forms of each may occur in suitable habitats (cf. V (b)). There is some evidence of large-fruited vigorous plants of higher chromosome number in Scandinavia, and similar plants may occur in Britain.

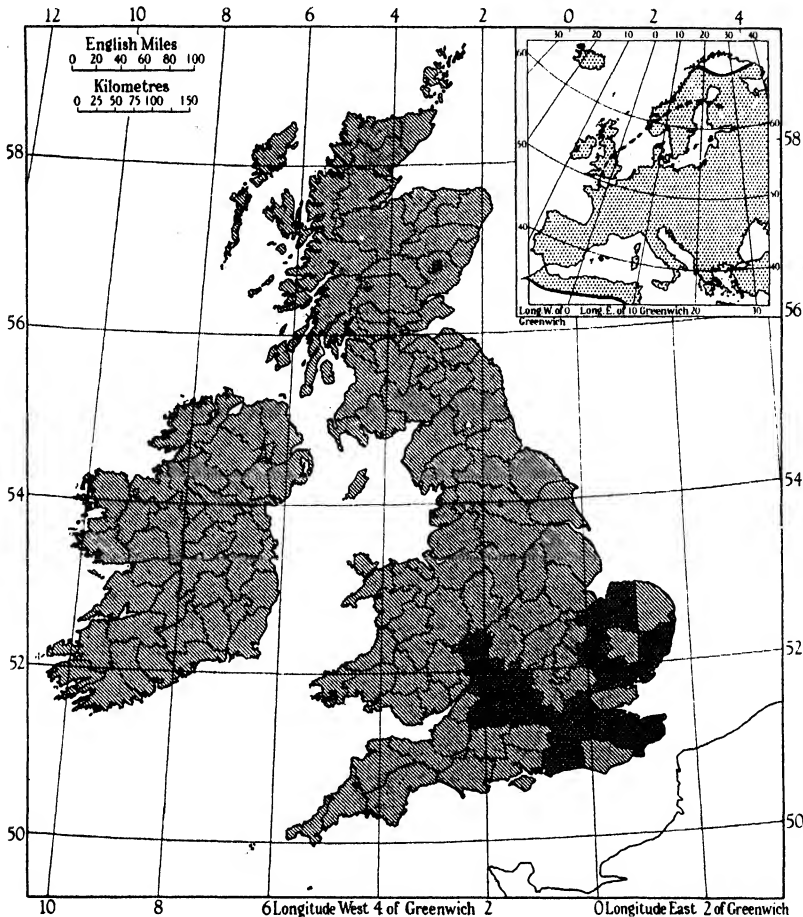


Fig. 1. *Eleocharis palustris* (L.) R.Br. em. R. & S. Vice-comital distribution in the British Isles and (inset) European distribution. ▨ subsp. *vulgaris* only recorded. ▩ subsp. *vulgaris* and *microcarpa* recorded. (Dotted line on inset map indicates approximate northern limit of subsp. *microcarpa* in Europe.)

var. minor auct. Small plants of either subspecies may be found under this varietal name.

var. arenaria Sonder. Coastal sand-dune plants, usually dwarf and with a well-developed rhizome, may be placed under this variety; it is probable that there is a genetic (ecotypic) basis to some of the characters exhibited by such plants.

var. glaucescens A. & G. Plants with strikingly glaucous stems have been found with normal green plants (e.g. subsp. *vulgaris*, coll. J. P. Brenan and N. D. Simpson, east Donegal, Ireland, 1938, in Herb. Simpson). Such variation clearly has a genetic basis.

The occurrence of the species in brackish marshes as well as inland suggests strongly that there is ecotypic variation with respect to salt resistance (cf. *E. uniglumis*). Cultivation experiments suggest also that there is genetic variation in plasticity as measured by haulm thickness in different habitats; but the very considerable variation in haulm length seen in different habitats has been shown by cultivation to be very largely phenotypic in origin.

II. *General distribution.* A native of Europe, common throughout the British Isles and locally dominant round shallow pools, in ditches, marshes, fens and wet meadows. The species ascends to 1500 ft. (460 m.) in Wales (*Comit. Fl.*); this record almost certainly refers to subsp. *vulgaris*, which is not infrequently found in the marginal communities of upland lakes and ponds (see below). All records for subsp. *microcarpa* as yet obtained are lowland.

The taxonomic complexity of the aggregate species '*E. palustris*' (i.e. the group *Palustres*) makes generalizations on the geographical and altitudinal distribution of the species difficult to make. It is clear, however, that the plant generally called *E. palustris* in southern and eastern Europe is subsp. *microcarpa*, whilst over the greater part of northern and western Europe subsp. *vulgaris* is common together with subsp. *microcarpa*. The *Palustres*, and probably the species *E. palustris* itself, occur throughout Asia and North America, in North Africa and India.

II. *Habitat.* *E. palustris* is a plant of shallow ponds and ditches, marshes and wet meadows. All the habitats are characterized by affording little or no competition with tall-growing species; it seems likely that an intolerance of shade is one of the most important factors limiting the species. The substratum may be peat or mineral soils with a high content of organic matter or sandy and gravelly soils on lake shores. The species exhibits a wide tolerance of water levels; it will grow in shallow water (up to c. 50 cm.), and at the other extreme will tolerate habitats where the water-table may be several cm. below soil-level in summer, although water at or above soil-level seems to be necessary during the spring period of active rhizome growth. The soils are normally alkaline or neutral, although the plant may be found on damp rather acid sandy soils; it is rarely if ever to be found on acid peat, however. There is no obvious difference between the two subspecies in their habitat requirements, although more information is required on the habitats of subsp. *microcarpa*.

III, IV. *Communities; response to biotic factors.* The plant is a characteristic dominant of the 'low reed-swamp' surrounding small ponds or fringing ditches (cf. Table 1, nos. 1-4). Such communities often give the impression of being of very recent origin, and there is much evidence to support the view that the plant is common in such habitats because of efficient dispersal and early colonization. Competition with taller species (e.g. *Juncus* spp.), as peat accumulation causes a rise in soil-level, may rapidly bring about a decline from dominance, but in many habitats where regular clearing of the aquatic vegetation is practised, the *Eleocharis* can persist as a dominant. The natural pools occurring in dune-slacks also afford habitats for *Eleocharis*, and a clear zonation is often developed, as, for example, at Ainsdale, west Lancashire, where a small pool had a central dominant *E. palustris* community, with a marginal *Salix repens* zone. Here the edaphic factors, causing drying out in the summer, may be responsible for the absence of taller growing reed-swamp species which would exclude the *Eleocharis*. In Scotland and northern England, upland lake-shore communities are often of a very 'open' nature, and the presence of the species is at least in some cases to be correlated with a minimum base supply in the water;

thus on the rather barren stony margin of Loch Tay at Fearnan, Perthshire, there was a flourishing stand at the point where a small stream from Ben Lawers enters the loch. (*E. pauciflora*, which will not tolerate base-deficient soils, was also confined to this small area of shore.) Very similar gravel-alluvium habitats were seen at the west end of Loch Mullardoch, east Inverness, where the plant was a reed-swamp dominant with *Carex rostrata* and *Glyceria fluitans*. Habitats in running water seem very rare; only one such community has been seen, in a small gravelly stream in Upper Teesdale, where the plant had no associated species.

The other type of habitat is that of marsh, fen or grazing pasture (cf. Table 1, nos. 5, 7-10); in these there is almost invariably some biotic factor operating to exclude the taller species, or to break and keep open the soil for the spread of the rhizomes. Thus on Wicken Fen, Cambs, the species is confined to the ditches, where it is a reed-swamp constituent surviving because of artificial clearing, and the main drove which is cut very regularly and subject to trampling. *Eleocharis uniglumis* and *E. pauciflora* also occur on the main drove (cf. Table 1, no. 9). In rough-grazing pasture, the species can be easily overlooked, particularly where heavy grazing may have prevented flowering (cf. *E. uniglumis*). The plant occurs quite commonly on coastal grazing marshes with slightly brackish water, often with *E. uniglumis* (cf. Table 1, nos. 11-13).

Table 1. *Eleocharis palustris* and *E. uniglumis*—associated species

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>Eleocharis palustris</i>	a.-l.d.	d.	a.-s.d.	l.s.d.	a.-l.d.	.	l.a.	l.a.	f.	a.	l.s.d.	a.	a.
<i>E. uniglumis</i>	f.-a.	.	.	f.	f.	.	.	a.	l.d.	l.a.	l.f.-l.a.	d.	a.
<i>Agropyron repens</i>
<i>Agrostis stolonifera</i>	.	.	f.	a.	a.	.	.	o.	.	.	.	+	+	+	.	l.a.	o.*	.
<i>Alopecurus aequalis</i>	.	.	o.
<i>A. geniculatus</i>	.	.	.	a.
<i>Angelica silvestris</i>	+
<i>Anthoxanthum odoratum</i>	o.-f.
<i>Apium graveolens</i>	o.	.	.	.
<i>A. nodiflorum</i>	r.	o.	.	+
<i>Aster tripolium</i>	r.	.	.
<i>Baldellia ranunculoides</i>	a.
<i>Bellis perennis</i>	+
<i>Blysmus compressus</i>	l.f.-a.	o.-f.	.	.	.
<i>Caltha palustris</i>	r.	.	r.	a.	.
<i>Cardamine pratensis</i>	r.	.
<i>Carex acutiformis</i>	f.
<i>C. distans</i>	f.	f.	.	.	.
<i>C. disticha</i>	l.f.	.	o.	a.
<i>C. divisa</i>	+	a.
<i>C. flacca</i>	a.	f.	+	.	o.	.	a.
<i>C. hirta</i>	f.	.	.	f.
<i>C. lepidocarpa</i>	f.
<i>C. nigra</i>	l.f.	o.
<i>C. otrubae</i>	f.	o.	.	.	+	f.	.	.	.
<i>C. panicea</i>	f.
<i>C. rostrata</i>	f.
<i>Centaurea nigra</i>	r.
<i>Cerastium vulgatum</i>	+	f.
<i>Cirsium arvense</i>	.	.	o.
<i>C. lanceolatum</i>	l.f.	o.
<i>C. palustre</i>	+
<i>Comarum palustre</i>	r.
<i>Cynosurus cristatus</i>	+	.	.	.	a.
<i>Deschampsia caespitosa</i>	.	.	.	o.	.	.	.	l.f.	.	o.

* *Agrostis stolonifera* 17, a glaucous variety.

Table 1 (continued)

	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>Eleocharis</i>	.	.	.	l.f.-a.
<i>multicaulis</i>
<i>E. pauciflora</i>	f.	.	.	o.
<i>Epilobium hirsutum</i>	+
<i>E. obscurum</i>	o.
<i>E. parviflorum</i>	r.	+	.	+
<i>Festuca pratensis</i>	+	f.-a.
<i>F. rubra</i>	o.	.
<i>Filipendula ulmaria</i>	r.	.	o.
<i>Galium palustre</i>	.	.	f.	.	f.	f.	.
<i>Geranium dissectum</i>	r.
<i>Glaux maritima</i>	o.	.	+
<i>Glyceria fluitans</i>	l.f.	.	f.	l.d.	a.	.	+
<i>G. × pedicellata</i>	+
(<i>G. fluitans</i> × <i>plicata</i>)
<i>G. plicata</i>	o.	.	.
<i>Holcus lanatus</i>	.	.	.	a.	.	.	r.	.	.	a.
<i>Hydrocotyle vulgaris</i>	.	f.	.	.	f.	o.	.	l.f.	.	f.
<i>Iris pseudacorus</i>	a.
<i>Juncus articulatus</i>	.	.	f.	a.	.	a.	r.	f.	.	a.	+	l.a.	.
<i>J. bulbosus</i>	f.
<i>J. compressus</i>	l.f.
<i>J. effusus</i>	+	*	f.
<i>J. gerardii</i>	d.	.	+
<i>J. inflexus</i>	l.a.	l.f.	.	o.	o.	+	+
<i>J. subnodulosus</i>	.	.	l.a.	.	.	a.	.	f.	.	.	+
<i>Lathyrus pratensis</i>	+	r.
<i>Leontodon autumnalis</i>	r.	+	.	r.	.	.
<i>Lolium perenne</i>	o.
<i>Lotus uliginosus</i>	o.
<i>Lycopus europaeus</i>	.	.	o.
<i>Mentha aquatica</i>	.	o.	.	.	o.
<i>Myosotis scorpioides</i>	+	r.
<i>Nasturtium officinale</i>	.	o.
<i>Oenanthe fistulosa</i>	a.
<i>Oe. lachenalii</i>	r.	.	.
<i>Orechis incarnata</i>	+
<i>Pedicularis palustris</i>	r.
<i>Phalaris arundinacea</i>	o.
<i>Phleum pratense</i>	r.
<i>Phragmites communis</i>	+	†
<i>Plantago lanceolata</i>	+
<i>P. major</i>
<i>Poa pratensis</i>	f.
<i>P. trivialis</i>	+	r.	o.	.
<i>Polygonum</i>	+	r.
<i>amphibium</i>
<i>Potamogeton</i>	r.
? <i>polygonifolius</i>
<i>Potentilla anserina</i>	.	.	.	o.	.	.	.	o.
<i>P. erecta</i>	r.
<i>Prunella vulgaris</i>	r.	.	r.	f.
<i>Puccinellia maritima</i>	a.	.
<i>Pulicaria dysenterica</i>	+	.	.	.	f.	+
<i>Ranunculus acris</i>	+	r.	a.
<i>R. flammula</i>	.	.	.	f.-a.	o.
<i>R. repens</i>	+	a.	.	f.
<i>R. sceleratus</i>	o.	.	.	.
<i>Rumex acetosa</i>	+
<i>R. conglomeratus</i>	.	.	o.	.	.	.	o.-f.	+
<i>R. crispus</i>	.	r.
<i>R. viridis</i>	+
<i>Samolus valerandi</i>	o.
<i>Scirpus fluitans</i>	a.

* *Juncus effusus* 1, dominant in outer zone of pond.† *Phragmites communis* 9, present as cut bases of plants only.

Table 1 (*continued*)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>S. maritimus</i>	+	.	l.a.	.	.	.
<i>S. tabernaemontani</i>	r.	.	.
<i>Senecio aquaticus</i>	+	f.-a.	.	.	o.	r.	.
<i>Sium latifolium</i>	+
<i>Sparganium erectum</i>	a.
<i>Symphytum officinale</i>	r.
<i>Taraxacum officinale</i>	o.
<i>Thalictrum flavum</i>	r.
<i>Trifolium fragiferum</i>	a.	.	.	+
<i>T. medium</i>	r.
<i>T. pratense</i>	r.
<i>T. repens</i>	r.	.	.
<i>Triglochin maritimum</i>	+	.	.	a.	f.-l.a.	+
<i>T. palustre</i>	r.	o.	a.	o.	.	.	+
<i>Utricularia minor</i>	a.
<i>Veronica beccabunga</i>	+
<i>Equisetum palustre</i>	o.	.	f.	.	f.
<i>Hypnum cuspidatum</i>	a.
<i>H. revolvens</i>	a.
<i>Sphagnum</i> sp.	a., l.s.d.
<i>Chara</i> sp.	+

Reed-swamp:

1. Pond, Bramhope, near Leeds (cf. Tansley, p. 595).
2. Fresh-water pond behind dunes, Ainsdale, west Lancs, 31. vii. 47.
3. Pond, Quy Fen, Cambs, 27. vii. 46.
4. Fresh-water pond on headland, Filey Brig, east Yorks, 20. viii. 46.

Marsh, fen, wet meadow:

5. Wet depression, East Winch Common, Norfolk, 2. viii. 46.
6. Derby Fen, near King's Lynn, Norfolk, 2. viii. 46 (cf. p. 193, 'zone 2').
7. Rough grazed marshy pasture, Dernford Fen, Cambs, 14. vi. 46.
8. Rough grazed marshy pasture, Hauxton, Cambs, 22. vii. 46.
9. Main drove, Wicken Fen, Cambs, 10. viii. 47.
10. Rough grazed marshy pasture, Hagley Pool, Berks, 14. vi. 47.

Coastal (and inland saline) habitats:

11. Disturbed marshy ground, Lymington Pier, south Hants, 6. ix. 46.
12. Ditch on Hacklinge Marshes, near Sandwich, west Kent, 17. ix. 46.
13. Ditch on Graveney Marshes, near Whitstable, east Kent, 16. ix. 46.
14. Rough grazed brackish marsh, Medway Estuary, Snodland, Kent, 2. ix. 47.
15. Salt spring in meadow, Marcham, Berks, 14. vi. 47.
16. Grazed estuarine marsh, Beaulieu, south Hants, 10. ix. 46.
17. Estuarine tidal marsh, Beaulieu River, east Inverness, 17. vii. 47.
18. Stony shore of Upper Loch Torridon, west Ross (E. C. Wallace), 24. vii. 47.

V. (a) *Gregariousness*. Always strongly gregarious, often in large stands (cf. VI (a), (c)).

(b) *Performance in various habitats*. The species exhibits a very considerable plasticity, and plants varying in size from a few cm. to more than 60 cm. can be produced by growing a cloned individual under the extreme conditions of grazed pasture and open water's edge. Haulm thickness in such cases may vary from less than 1 to 6-8 mm. (diameter). The

production of tufts or rhizomes is strongly influenced by conditions of habitat; it is clear that the presence of standing water in spring induces an extensive rhizome development which may be very largely suppressed in drier conditions, when the whole of the living plant may be caespitose (cf. VI (a), (c)).

(c) *Effect of frost, drought, etc.* Perennating buds very frost-resistant; thus, no plants were lost in outdoor cultivation at Cambridge, either in pots or in the soil, during the very hard winter of 1946-7. No direct information available on drought-resistance, but the plant is absent from soils which dry out in summer, and rhizome growth seems to be dependent on water at the soil surface in spring.

VI. (a), (c). *Morphology; perennation.* The rhizome is structurally a sympodium, although apparently monopodial, growing forward horizontally a few cm. below the soil surface, and giving off in association with each node an erect haulm. (A detailed description of the vegetative morphology of *Eleocharis* is being prepared for publication elsewhere.) Adventitious roots arise from each nodal region and bear a large number of very short laterals. In spring active rhizome growth begins early (in March or April in England), and normally continues throughout the summer if sufficient water is present. Tufts of haulms arise from a bud at the base of each primary haulm of the rhizome; these tufts may become rhizomes if the main rhizome is damaged, or in especially favourable conditions of growth in water. In the autumn rhizome growth ceases, and the growing point and all subsidiary growing points which have arisen from the development of the buds at the haulm-bases may perennate. During the second year the links of the rhizome chain begin to decay, and the older tufts function as independent units. In water the rhizomes may be very vigorous and cover several square metres in a single season's growth; in grazed pasture, on the other hand, most of the growth in any normal season will probably be caespitose, and strongly tufted plants with short dead rhizome chains are common in such habitats. Observation of many natural populations suggests strongly that over a considerable area (a single pond, ditch or damp area in grazed pasture) the plants have originated vegetatively from a single individual; although populations are known which can be divided on fruit characters into two types, presumably genetically different and of independent origins.

(b) *Mycorrhiza.* No information.

(d) *Chromosome number.* $2n=38$ for type material of subsp. *vulgaris* from Hauxton, Cambs; confirmed by material from a wide variety of British localities. Doxey (1938) found $2n=38$ and 39 for several different *E. palustris* plants from northern English localities, also single plants with $2n=37$ and 40-41. Håkansson (1928, 1929) had $2n=38$ for Swedish material.

$2n=16$ for type material of subsp. *microcarpa* from Graveney Marshes, near Whitstable, east Kent; also from Hagley Pool, Berks (with subsp. *vulgaris*, $2n=38$). Doxey (1938) gives $2n=16$ for material from River Thames, Kew. Håkansson (1929) found $2n=16$ for plants from south Sweden.

VII. *Phenology.* The simple terminal spikes of flowers are borne on haulms arising usually from the tufts in May or early June. The main flowering period is short and closely synchronized for any one population, but there is often a second and smaller flowering period in late summer, especially where the plants are subject to grazing. The spike rudiments are distinguishable in the young haulms on dissection of the perennating growing points during the resting stage in winter, and must be laid down the previous autumn. Only a limited number of haulms produce spikes; those which precede and follow

the flowering ones at any one growing point possess only the vestiges of a terminal spike (in the form of the two basal glumes, which are represented by tiny structures visible with a lens), but a few intermediates with very poorly developed spikes may occur. The production of spikes seems to depend on factors of internal and external environment. Thus very few plants flowered in their first year after planting out at the water's edge, but nearly all flowered in their second year. Shade and aquatic conditions both seem to discourage flowering.

VIII. (a) *Floral biology*. The flowers are protogynous, and pollination is by wind. There is no evidence of apomixis, and cross-pollination between flowers of the same or different spikes is normal.

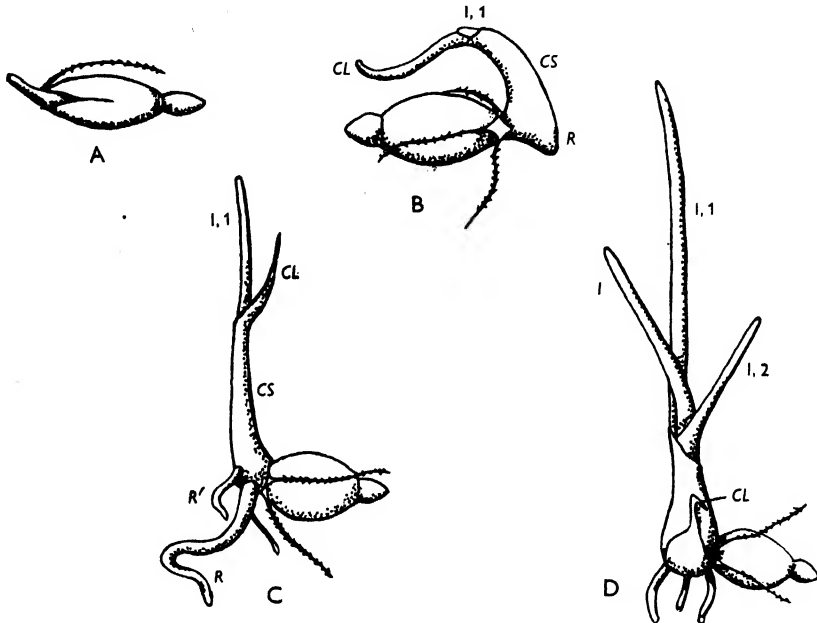


Fig. 2. Stages in germination of *Eleocharis palustris* fruits. A ($\times 16$). 24 hr. after germination, with cotyledon tip emerging. B ($\times 16$). 2-3 days after germination. Cotyledon sheath (CS), cotyledon lamina (CL), tip of first foliage leaf (I, 1), developing primary root (R). C ($\times 12$). 7 days old. First foliage leaf well developed, cotyledon lamina withering; adventitious roots (R') developing. D ($\times 12$). About 28 days old. Tip of primary shoot (I), and two foliage leaves (I, 1 and I, 2), fully developed.

(b) *Hybrids*. Such few attempts at hybridization as have been made have proved unsuccessful, and no putative hybrids between the two subspecies have been seen in the field. Although more investigation is needed, it seems probable that the two subspecies are genetically effectively isolated. The status of certain apparently fertile morphological intermediates between *E. palustris* and *E. uniglumis* needs further investigation.

(c) *Seed production and dispersal*. Fruit (a single-seeded nut) is set abundantly; spikes commonly contain 15-30 fruits in subsp. *vulgaris*, and 20-40 in subsp. *microcarpa*—i.e. a considerable proportion, often about one-half, of the flowers set fruit. The barbed bristles at the base of the nut are assumed to have significance in dispersal. Ridley (*Disp. Plants*, pp. 492-3) gives evidence for the importance of ducks in dispersal of *Eleocharis* (presumably *Palustres* species) in North America; large quantities of the fruits were found in the stomachs of the shot birds examined. In this country the success with which newly dug ponds or ditches are colonized suggests that fruit dispersal is very efficient.

(d) *Viability of seeds; germination.* No information on viability. No seedlings have yet been found in nature, but the fruits germinate in the laboratory after a dormancy period of several months. Percentage germinations as high as 80–90 have resulted from fruit samples placed on damp filter-paper in Petri dishes in autumn and left for about 6 months; in these cases germination begins rather suddenly and is soon complete.

(e) *Seedling morphology.* The young seedling 2–3 days after germination (Fig. 2B) has a cotyledon consisting of sheath (CS) and setaceous lamina (CL); the primary root (R) is just developing. After about 7 days (Fig. 2C) the root (R) is well established, but is already being superseded by adventitious roots (R'). The first foliage leaf (I, 1) is well developed. A later stage (Fig. 2D), about a month old, shows the primary haulm fully developed, consisting of the cotyledon, two foliage leaves with cylindrical laminae, and the tip of the haulm which has most recently emerged from the sheaths of the leaves. Adventitious roots have superseded the primary root. In later stages a spiral succession of haulms is produced by development of buds axillary to the leaf-sheaths; and finally the growing-point bends over to give the rhizome. (A detailed account of seedling and adult morphology is being prepared for publication elsewhere.)

(f) *Effective reproduction.* The field evidence suggests that, after an initial chance colonization, presumably by seed, of a suitable new habitat (e.g. a newly dug pond or ditch), the subsequent rapid spread of the plant is almost entirely by rhizome (cf. VI (c)).

IX. (a) *Animal feeders and parasites.* Only one record has been traced, viz. larvae of *Bactra furfurana* Haw. (Micro-Lepidoptera) on stems of *Eleocharis palustris*. (Note on specimen ex herb. Bennett, in Herb. Mus. Brit.)

(b), (c). *Plant parasites and saprophytes; diseases.* The commonest and most conspicuous parasitic fungus is the ergot *Claviceps nigricans* Tul., which produces black sclerotia in the ovaries, and may so seriously attack a population as to make it impossible to find a normal fruit. A plant from such a heavily infected population, when brought under cultivation, produced normal fruit with no sign of the parasite in the following season. Other recorded fungi are:

ASCOMYCETES: DISCOMYCETES: *Pyrenopeziza fecunda* (Phill) Sacc.

PYRENOAMYCETES: *Myiocopron Heleocharidis* Grove

FUNGI IMPERFECTI: COELOMYCETES: *Ascochyta decipiens* Trail, *Conothyrium scirpi* Trail, *Hendersonia norfolcia* Sacc., *Stagonospora aquatica* Sacc. var. *quinqueseptata* Grove (*S. scirpi* Tehon), *S. Heleocharidis* Trail.

The list is compiled from the following sources: *Br. Rust. F.*, Sacc. *Syll.*; Grove, W. B. (1930), *J. Bot.* **68**, 133; Tubeuf, K. & Smith, W. G. (1897), *Diseases of Plants*.

X. *History* (from information supplied by H. Godwin). Subfossil fruits of *Eleocharis palustris* are stated to occur in Early Glacial and Interglacial deposits in England (Clement Reid). They have also been recorded in the Late Glacial Taplow terrace deposits at Euston; in Irish Late Glacial (Allerød) deposits, associated with *Cervus megaceros*, at Ballybetagh and elsewhere; in 'moorlog' from the North Sea floor (probably Early Post-Glacial), and in shell-marl at the base of deposits in Linton Mires, Wharfedale, Yorks, also Early Post-Glacial. A later post-glacial record is from the submerged forest peat of Bideford Bay (Inkerman Rogers, see Reid, 1913, p. 64).

First record in Britain ('*Juncus aquaticus minor capitulis Equisete*') in Johnson's edition of Gerard's *Herbal* (1633).

L.C. (Ed. 11) No. 1989

***Eleocharis uniglumis* (Link) Schult.**

S. M. WALTERS

Differs from *E. palustris* as follows:

Haulms and rhizomes always slender (even in favourable conditions of growth); rhizomes usually more strongly developed and tufts smaller. Leaf-sheaths at base of haulms more deeply reddish purple in colour. Spikes fewer-flowered (15–30), with usually a single sterile glume surrounding spike at base. Style-base of fruit rather broad, often

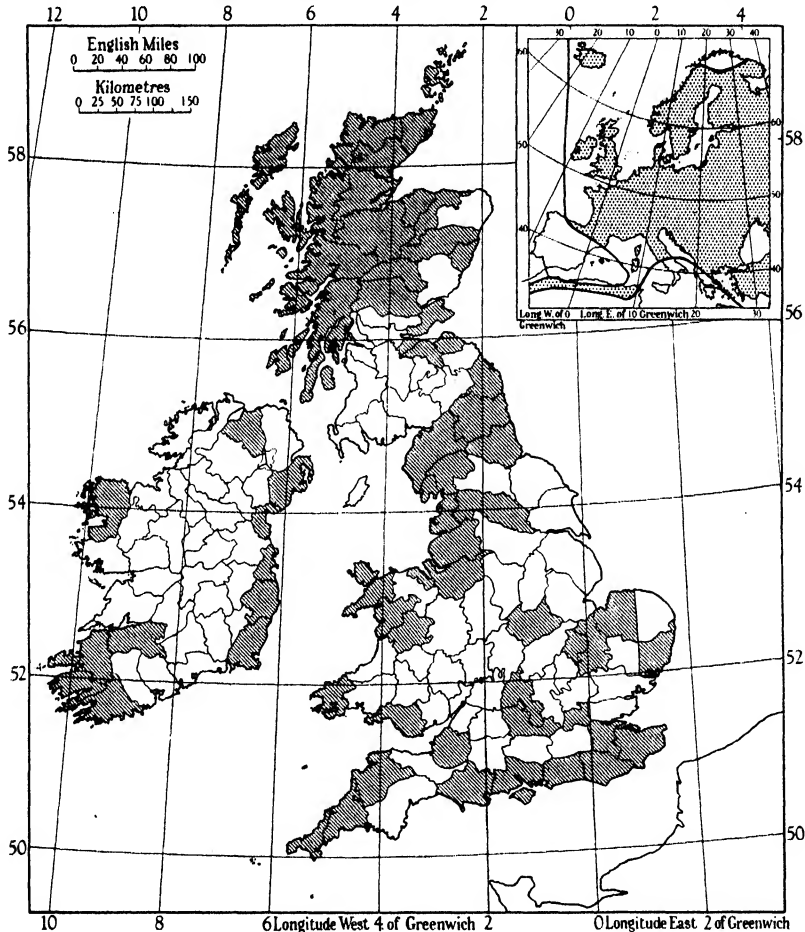


Fig. 3. *Eleocharis uniglumis* (Link) Schult. Vice-comital distribution in the British Isles and (inset) European distribution.

broadier than long; bristles 4(5), often in British material shorter than fruit; fruit surface usually more strongly and coarsely punctate under lens.

E. watsoni Bab. was distinguished from *E. uniglumis* by its author on fruit shape, the possession of a punctate-striate fruit surface, and bristles shorter than the fruit; but in none of these characters does it differ sufficiently from *E. uniglumis* (with which it seems

Babington was not well acquainted) to be worthy even of varietal rank. The type material of *E. watsoni* is a very small coastal *E. uniglumis*; later collections referred to *E. watsoni* have been of plants with short bristles and strongly punctate fruit. Lindberg (1902), noting variation in bristle length in both *E. uniglumis* and *E. palustris*, divided each with respect to this character into several formae, of which the extremes are f. *typica*, with bristles exceeding fruit, and f. *nulliseta*, with no bristles. A similar, undoubtedly genetic, variation is found in both species in Britain; 'forma *subnulliseta*', with very undeveloped bristles, is not rare in British *E. uniglumis*.

Good evidence for ecotypic differentiation is afforded by saline cultivation experiments, in which coastal plants showed a distinctly higher salt tolerance than inland ones (although the latter themselves were very tolerant). No evidence of other ecotypes has been shown by cultivation experiments in different water-levels.

A native of Europe, locally abundant in the British Isles in brackish coastal and estuarine marshes and grazing meadows, but also occurring inland.

I. *Geographical and altitudinal distribution.* The species is widespread in the British Isles, but the details of its distribution are very imperfectly known. The plant has undoubtedly been overlooked, particularly in inland habitats, and its absence from many vice-counties on the distribution map is very unlikely to be real. The west Scottish records for *E. uniglumis* refer in most cases to plants which are in some respects intermediate between this species and *E. palustris*, and whose status has not yet been determined.

The European distribution, though very imperfectly known, seems to show a real southern and western limit. Over the whole of northern Europe the species is widely distributed in coastal and inland habitats; it is absent from Portugal and most of Spain, and apparently confined to mountain habitats in north Italy, Greece and the Balkans. It is also recorded for North Africa (Algeria and Morocco), throughout Asia and North America.

A lowland species in Britain; only one locality is yet known in any upland habitat—Malham Tarn, Yorks, c. 1250 ft. (390 m.). On the Continent, however, it occurs on mountains, and has been recorded from nearly 2000 m. in central Europe (Koch, 1907).

II. *Habitat.* Three kinds of habitat may be distinguished, of which the commonest is estuarine flats, sand-dune slacks, or brackish grazing marshes. It is, however, by no means rare inland, occurring in lowland fen or grazing pasture, often with *E. palustris*. The third type of habitat, upland calcareous marsh, is probably rare in Britain, for as yet only one such locality is known (Malham Tarn, Yorks). In Sweden, however, very similar calcareous marsh localities are more numerous. The species is found on a wide range of soils from alkaline peats to saline sands or gravels. Unlike *E. palustris* it is rarely if ever found in a typical reed-swamp habitat, and seems to grow badly in water, unless very shallow. Saline or slightly to strongly alkaline soils seem to be necessary for its growth. In all habitats, with the exception of a few tidal estuarine ones (cf. Table 1, no. 17), the plant is commonly found growing with *E. palustris*.

III, IV. *Communities; response to biotic factors.* Almost pure communities of the species may occur in tidal marshes in river estuaries. Thus in the estuary of the Beaulieu River, east Inverness (cf. Table 1, no. 17), there was a band of closed vegetation about 30 m. wide in which the species was completely dominant; in the lower zone of this, next to the low-water channel, the only associated species were *Triglochin maritimum* and a glaucous variety of *Agrostis stolonifera*. Similar, but much less luxuriant, estuarine zones of the

species have been seen elsewhere, as in the Beaulieu River estuary, south Hants (cf. Table 1, no. 16); but it is rare to find an ungrazed community, as the east Inverness one. In coastal grazing marshes, the plant is a frequent constituent of the short turf, and commonly lines the drainage ditches, where growth may be more luxuriant (cf. Table 1, no. 13). An inland salt spring near Marcham, Berks (cf. Table 1, no. 15) had a very clear zone of dominant *Juncus gerardii*, in which *Eleocharis uniglumis* was very luxuriant and locally abundant. In more normal inland habitats, of marshy pasture and fen, the species list may be rather large, as in the Derby Fen, Norfolk, locality (cf. Table 1, no. 6), and p. 193, 'zone 2'). The occurrence of the species on the main drove of Wicken Fen, Cambs (cf. Table 1, no. 9), is interesting in that it emphasizes the necessity for disturbed and artificial habitats. In heavily grazed pasture, it may be extremely difficult to detect the species, and, in the absence of spikes, to distinguish it from *E. palustris*; it is certain that it is much commoner inland than is generally supposed.

V. (a) *Gregariousness*. Highly gregarious, as *E. palustris*.

(b) *Performance in various habitats*. The plasticity of the species has been shown by cultivation to be very much less than that of typical *E. palustris* (both subspecies), a fact with which may be correlated its absence from reed-swamp communities. Salt tolerance has also been tested by cultivation experiments; the results showed that *E. uniglumis* from inland non-saline habitats tolerates saline soil water at least as well as coastal *E. palustris*, and very much better than inland *E. palustris*. A dilute saline solution (up to 1 in 10 sea water) has little or no harmful effect, only a slight stunting being noticeable. The dominance of the plant in estuarine communities is undoubtedly in part due to the suppression of other competing species by the salt water. As in *E. palustris*, caespitose or rhizomatous growth is largely determined by environmental conditions; but the balance is more strongly in favour of rhizome production, and, under the same conditions of growth, the plant will produce a greater rhizome system and smaller tufts than *E. palustris*.

(c) *Effect of frost, drought, etc.* Remarks under *E. palustris* apply here.

VI. (a, c) *Morphology; perennation*. Remarks on general morphology and mode of perennation under *E. palustris* apply also to this species. The rhizome, however, is normally more slender, and runs much nearer the soil surface; thus in Wicken peat it is usually 1–2 cm. below the surface whilst *E. palustris* in the same conditions is 4–6 cm. It is possible that the species is generally more sensitive to aeration deficiencies and less tolerant of badly aerated rooting media than *E. palustris* (cf. absence from reed-swamp habitats).

(b) *Mycorrhiza*. No information.

(d) *Chromosome number*. Material from Graveney Marshes, near Whitstable, east Kent, and from Derby Fen, Norfolk, has given $2n=46$. Doxey (1938) found the same diploid number for *E. uniglumis* from a coastal locality near Southport, Lancs. Evidence of cytological irregularity has been found in a west Kent plant, which gave haploid numbers varying from $n=19$ to 24 in the pollen-grain mitoses, and to a lesser extent in other plants. Håkansson (1929) gives $2n=46$ for Swedish material; other European counts for plants identified as *E. uniglumis* are $2n=16$ and 32 (cf. Löve & Löve, 1948).

VII. *Phenology*. Details given under *E. palustris* apply—except that the terminal spike vestige on the vegetative haulm shows the single basal glume characteristic of the species.

VIII. (a) *Floral biology*. As *E. palustris*.

(b) *Hybrids*. See *E. palustris*.

(c) *Seed production and dispersal.* Fruit usually less abundant than in *E. palustris*; the spike contains fewer flowers, and frequently only a small number set good fruit. Remarks on dispersal under *E. palustris* apply here.

(d) *Viability of seeds; germination.* No information on viability. A sample of fruit tested in the manner used for *E. palustris* gave 20% germination, with a similar dormancy period of about 6 months.

(e) *Seedling morphology.* Seedlings rather slenderer than those of *E. palustris*, otherwise identical.

(f) *Effective reproduction.* As in *E. palustris* a single presumably seedling colonization is followed by extensive vegetative spread.

IX. (a) *Animal feeders or parasites.* No information.

(b), (c) *Plant parasites; diseases.* *Claviceps nigricans* occurs, as in *Eleocharis palustris*. No records of this species as host plant as distinct from '*E. palustris*' have been found.

X. *History* (from information supplied by H. Godwin). Subfossil fruits have been reported from the Late-Glacial deposits at Barnwell Green, Lea Valley, and also from the later Post-Glacial in upper shore peat at Leasowe, Cheshire, and in shore peat on the south-west Lancashire coast.

The work involved in the preparation of these accounts of *Eleocharis* was done whilst the author was receiving a Maintenance Allowance from the Department of Scientific and Industrial Research.

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ARUM L.

L.C. (Ed. 11) No. 1924

Arum maculatum L.

F. A. SOWTER

A robust, somewhat fleshy perennial, 15–40 cm., with 4–6 radical leaves springing from a stout whitish corm. Leaf lamina hastate, with deflexed lobes, shining, with irregular black to purple blotches or uniformly green; veins pinnately branched, sometimes whitish; petiole channelled above, 10–20 cm. Flowers monoecious, protandrous, crowded on a

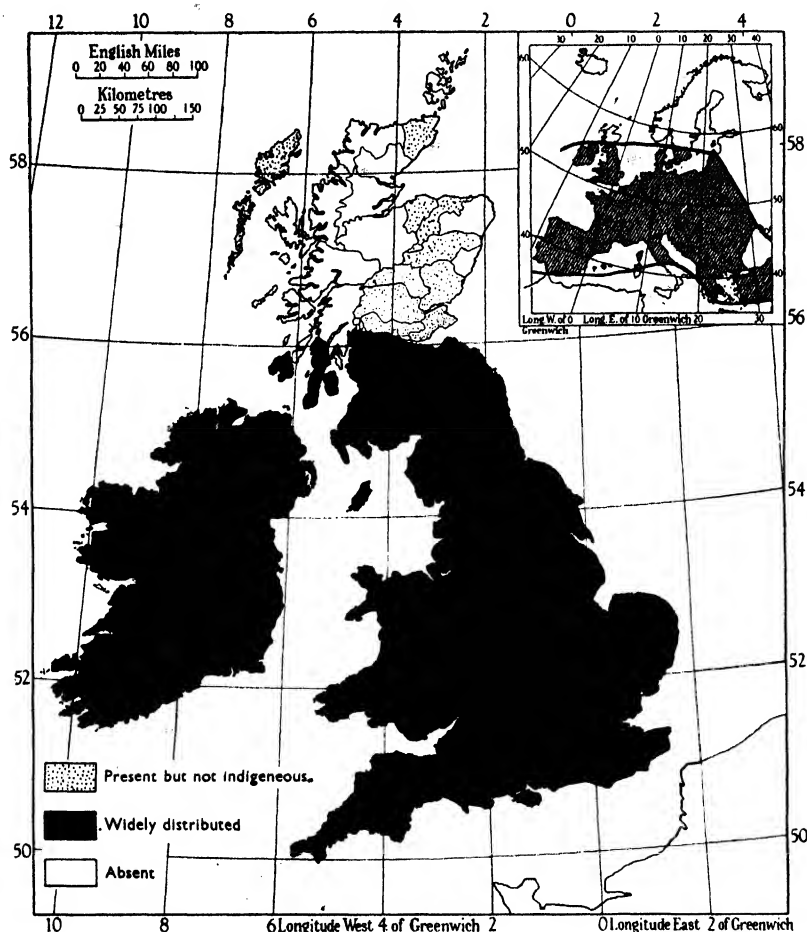


Fig. 1. *Arum maculatum* L. Vice-comital distribution in British Isles and (inset) distribution in Europe.

vertical axis prolonged as the purplish or yellowish club-shaped spadix (5–6 × 0.5–0.7 cm.). Spathe cowl-shaped, tapering, convolute with overlapping edges at the base, open at the base of the spadix, shrivelling after flowering, spotted or uniformly green, 10–25 cm. long. Inflorescence axis bearing (in order from the base of the spadix downwards): (a) a zone of 30–40 deflexed hairs, 4–5 mm. long; (b) a zone of c. 100 sessile purplish red to yellow anthers,

1–1.5 mm. long, dehiscing longitudinally, mostly arranged in pairs; (c) 30–50 pale yellow syncarpous unilocular ovaries, 3 mm. long, with short style and entire stigma; the highest row are sterile and have terminal filamentous processes. Perianth and nectaries none. Infructescence a bare spike of berries, scarlet when ripe, containing 1–4 reticulated, globose seeds (6×5 mm.).

Plants with spotted leaves (f. *maculatum*) and those with unspotted leaves (f. *immaculatum*) grow together in similar habitats. The variety *tetreltii* Corb. has a yellow spadix, but plants may be found showing intermediate spadix colours. The dark patches on the leaves of the spotted form are due to a purple anthocyanin (Wheldale, 1916). Stahl (1896) suggested that the anthocyanin of this and other shade plants increases the absorption of heat by the leaves and thus promotes transpiration. Often the marking corresponds with a prominent elevation or depression and both may be found on the same leaf.

The frequency and distribution of spotted and unspotted plants in Britain is extremely variable, but Pethybridge (1903) concluded that in England, as in Ireland, spotted plants are much more uncommon than unspotted. A count made by Phillips (1903) at Graign-managh, Ireland, showed a proportion of spotted to unspotted plants of 1:500, but counts by the present writer in the Midlands gave a proportion of 1:4.88. Bromfield (1856) states that the unspotted plant is rarer in the north.

A lowland species of woods, hedgebanks and shady places widely distributed throughout England, Wales, Ireland and southern Scotland.

I. *Geographical and altitudinal distribution.* Recorded for all English vice-counties. Much planting has occurred in Scotland, but it extends northwards as a native species to a line approximating the River Forth to Argyle. North of this limit it is generally considered naturalized. It is doubtfully recorded for west Perth with Clackmannan (87), mid-Perth (88), south Aberdeen (92), Banff (94), Moray (95) and Caithness (109). There are also records from east Perth (89) and Angus (90). In the latter vice-county it grows in a shrubbery at Parkhill near Arbroath, where it has probably been planted (U. K. Duncan). Campbell (1936) records it for North Uist (110) 'under wall, outside a garden'. It is abundant at Finlarig Castle, Killin, Perthshire (88), but not native (White, 1898). Although noted as 'doubtful' from Fife with Kinross (85) (*Comit. Fl.*), it is recorded from eleven localities in this vice-county (Young, 1936). Recorded for all Irish vice-counties, but it is generally rarer in the west than in the east (*Ir. Top. Bot.*), its north-western limit being reached in the Donegal Bay area (*Bot. Irl.*). In the Channel Islands it occurs in Jersey (Babington, 1839), Guernsey, Sark and Jethou. Absent from Alderney, Herm, Lihou and Crevichon (Marquand, 1901). Widely spread over southern and central Europe, northwards to southern Sweden (lat. 58° N.) (absent from Norway), and eastwards to Poland, the Carpathians and the Caucasus, where it is replaced by *Arum orientale*. It is cited for Turkey (*Cyb. Brit. Compendium*); the Balkan Peninsula southwards to Peloponnesus; in Italy to the centre of the peninsula. Also in Spain and, according to Watson, crossing to Algeria (lat. 35° N.), but Battandier & Trabut (1902) do not record it for Algeria and Tunis and say that *A. italicum* has been recorded in the past as *A. maculatum*. Jahandiez & Maire (1931, 1934) say it is absent from Morocco, but mention that it has been recorded in error. Thus it seems absent from North Africa. Its frequency is variable. In central and western France it is common, widespread in Belgium and Holland, whilst in certain parts of Germany it is quite absent (e.g. East Mecklenburg and Prussia) (*Lebensg.* 1, iii, p. 33).

In England ascends to 1350 ft. (411 m.) on Thornthwaite Scar, above Brough (Wilson,

1938); 1200 ft. (365 m.) on Leck Fell, west Lancs; 1050 ft. (320 m.) in Derbyshire (West); 980 ft. (298 m.) in Teesdale; 750 ft. (228 m.) Buckden, Craven-in-Wharfedale (Lees, 1937). 1500 ft. above Llanthony, Black Mountains, Monmouthshire (E. W. Jones). In Wales 1000 ft. (304 m.) or higher on Llansannan, Denbigh (A. A. Dallman). In Ireland to 1000 ft. (304 m.) in the Mourne (*Alt. Range Br. Pl.*). In Europe it ascends to about 1000 m. (Switzerland to 1050 m.) (Hegi, *Fl.* 2, 133). In the Swiss Jura it is recorded at 710 m. at La Clochette and 810 m. at Vers-chez-les Blanc (Bonner, 1940). In Canton Graubünden (Switzerland) it occurs only in the beech region at 500–600 m. (Braun-Blanquet & Rübel, 1932).

II. *Habitat.* (a) *Climatic and topographical limitations.* In deciduous woods, coppices, fox coverts, plantations, hedgerows, hedgebanks, scrubs, thickets, orchards, gardens, on wooded cliffs, and occasionally amongst the ground vegetation of marsh formations (alder-willow association). In dense woods it becomes marginal. For optimum growth it requires a moist, loose soil, well supplied with humus. It seems to be equally abundant in woodland of long standing as in woods which are only 100–140 years old. Light intensity determinations (actinometer) were made in Selsdon Wood, Surrey, by C. T. Prime (1943) during the period of its active growth (March), and they showed that on a fine sunny day, the average intensity inside the wood was 50% of the light outside the wood, but on an overcast day the average intensity inside the wood was 95% of the light outside the wood. The humidity was determined at the same time and showed the relative humidity to be 73% in the wood, and 61% outside the wood.

(b) *Substratum.* It is found on a wide variety of soils of high base status including sand, loam and calcareous soils but is absent from acid peaty ground. It tolerates considerable moisture but also grows on very porous highly drained soils. Soil samples were examined from the following localities:

(i) Ravensdale, Derbyshire, on very stony limestone slopes amongst scrub with a humus layer $\frac{1}{2}$ –1 in.

(ii) In Leicestershire on a heavy clay soil mixed with the 'Brand' series of slates the corms were found 3 in. down. There was a sparse layer of dead leaves.

(iii) In a mixed coppice (oak-ash) on a dark clay for $5\frac{1}{2}$ in. (corms) and then becoming lighter:

	(i)	(ii)	(iii)
Water content (%)	46.3	16.8	22.5
Humus content (%)	23.6	6.74	6.64
Nitrates	+	—	—
Base deficiency (Comber)	—	—	—
Carbonates (HCl test)	+	—	—
pH (electrometric)	6.1	6.1	5.7

Its tolerance of wet conditions is shown in Bishop Wood, near Selby, Yorks (alder-ash-elm) on Warp Clay. Soil a grey clay, with winter water-table at about 4 in. from surface. Summer water-table absent. Very high exchangeable calcium content but very low K and PO_4 , pH of surface soil, 4.68; pH at 24 in., 6.58. The following figures (E. W. Jones) illustrate the limitations in soil: In Dorset on chalk it is recorded in 16 out of 133 stands; of these 6 out of 16 occurrences are on shallow chalk soils, and none on flint gravels or deep clay-with-flints. On Tertiary strata it is present in 1 out of 54 stands; this was in a planted stand of relatively recent origin on former arable soil and was associated with other calcicoles. In the Chilterns (Watlington) it is recorded in 2 out of 44 stands on clay-with-flints on the plateau, and in 8 out of 9 stands on chalk soils of steep slopes. At

Symonds Yat, Monmouthshire (High Meadow Woods) it is recorded in 75 out of 147 stands on Carboniferous Limestone, in 17% of the stands on Old Red Sandstone (when it is local and confined to moist valley bottoms), and in 4 out of 100 stands on Coal Measure loams. In Wales and the Lake District, on Silurian and Ordovician shales, it is a very local plant and in general is present in less than 1% of the stands. In the beech woods of the Cranham Common-Painswick district (Cotswolds, Jurassic limestone) it is present in 43% of the stands. It invades abandoned arable land as shown by its presence in the interior of the oak-hazel wood succession in 1914 on the Broadbalk Wilderness at Rothamstead (Herts), abandoned in 1882 (Tansley, *Br. Isl.*). In ashwoods on limestone pavement it is an occasional species. B. L. T. de Silva (1934) examined thirteen soil samples from various woodlands in Kent where *A. maculatum* is present. These showed that it grows in soils rich in exchangeable calcium even when calcium carbonate is absent. His observations gave a range of exchangeable calcium from 4.5 to 19.9 m.equiv. with an average value of 12.3, whilst the pH values ranged from 5.9 to 7.0 with an average value of 6.4.

III. *Communities.* (a) Deciduous woodlands. In Britain in pedunculate damp oak-woods on heavy soils, it is a common associate of *Mercurialis perennis* provided that the Mercury shoots are not too dense (Tansley, *Br. Isl.*). Swamping by these shoots is suggested by the description (Jones, 1944) of the ground flora of a 30-year-old hardwood plantation on calcareous grit near Oxford where the dominant *M. perennis* forms a 20–100% cover and *Arum maculatum* is recorded as 'rare'. Other important associates of this species are: *Corylus avellana*, *Scilla non-scripta*, *Oxalis acetosella*, *Ranunculus ficaria*, *Anemone nemorosa*, *Ajuga reptans*, *Galeobdolon luteum*, *Primula vulgaris*, *Sanicula europaea*, *Asperula odorata*, *Potentilla sterilis*. In an oak (pedunculate) and *Fraxinus* wood in Ireland where the limestone lies practically bare, it occurs with *Quercus* and *Corylus avellana* (co-dominants), *Anemone nemorosa*, *Viola reichenbachiana*, *Oxalis acetosella*, *Geum urbanum*, *Circaea lutetiana*, *Viburnum opulus*, *Veronica chamaedrys*, *Prunella vulgaris*, *Neottia nidus-avis*, *Epipactis atropurpurea*, *Scilla non-scripta*, *Carex sylvatica*, *Polystichum setiferum*, *Dryopteris filix-mas* (*Bot. Irl.*). In sessile oakwoods on damp soil with mild humus with an undergrowth of *Rubus* spp., *Rosa* spp., *Crataegus oxyanthoides*, *Hedera helix*, *Lonicera periclymenum*, the field layer contains *Mercurialis perennis*, *Ranunculus ficaria*, *Anemone nemorosa*, *Deschampsia caespitosa*, *Holcus mollis*, *Digitalis purpurea*, *Melandrium dioicum*, *Stellaria holostea*, *Teucrium scorodonia*, *Pteridium aquilinum*, *Glechoma hederacea*, *Ajuga reptans* and *Rumex acetosella*.

At Carrickreagh, Ireland, ridges of bare limestone rise from the shore of Lough Erne and are covered with scrub which is continually cut. *Quercus sessiliflora* is sometimes dominant, sometimes *Betula pubescens*, and sometimes *Corylus* with much *Fraxinus*, *Viburnum opulus* and *Prunus spinosa*. *Arum maculatum* is present in the field layer with *Aquilegia vulgaris*, *Rubus saxatilis*, *Lysimachia nemorum*, *Prunella vulgaris*, *Epipactis helleborine*, *Scilla non-scripta* and *Pteridium aquilinum* (*Bot. Irl.*). It is less frequent in *Quercus sessiliflora* woods than in pure *Quercus robur* or *Fraxinus-Quercus robur* woods.

(b) Composition of communities in oak woods. (see Table 1).

(1) Malvernian and Uriconian formation: light clayed loams, occasionally fairly stiff clays; low humus content and water content may be low in dry weather.

(2) Woods of May Hill Sandstone on a loamy clay, generally acidic.

(3) Wenlock limestone: Rock has high percentage of calcium carbonate but surface soil leached (lime content less than 1%).

(4) Aymestry limestone: Limestone nodules interbedded with shales. Lower lime content than the Wenlock limestone. Leaching of surface layers reduces lime content to usually less than 1%.

(5) In oak-hornbeam woods of Hertfordshire (Salisbury, 1916, 1918) it is included amongst the commonest species of the shade flora in a mixed society, occupying the transition region between a damp society dominated by *Mercurialis perennis* and a dry society dominated by *Anemone nemorosa*.

Table 1. *Communities with Arum maculatum*

Field layer ...	(a) Oakwoods				
	1	2	3	4	5
<i>Arum maculatum</i>	o.	l.c.	f.-c.	l.f.	o.-l.c.
<i>Ajuga reptans</i>	+	+	f.-c.	o.-f.	l.f.-l.c.
<i>Alliaria petiolata</i> (margin)	f.	r.	f.	+	.
<i>Allium ursinum</i> (flushes)	.	l.ab.	l.f.	l.c.	.
<i>Anemone nemorosa</i>	l.c.	c.-l.ab.	c.	l.c.	r.r.-l.c.
<i>Angelica sylvestris</i> (flushes)	+	l.f.	+	o.	.
<i>Anthoxanthum odoratum</i>	f.	o.-f.	?	+	.
<i>Arctium vulgare</i>	c.	+	o.-f.	f.	r.r.
<i>Arenaria trinervia</i> (margin)	f.-o.	+	+	o.	r.
<i>Arrhenatherum elatius</i> (margin)	f.	f.	f.	f.	.
<i>Asperula odorata</i>	+	f.-r.	f.-l.ab.	o.-f.c.	r.r.-l.f.
<i>Brachypodium sylvaticum</i> (margin)	o.	f.	f.-c.	f.-c.	.
<i>Bromus ramosus</i>	r.r.	r.	o.-f.	o.	.
<i>Campanula trachelium</i>	r.	r.	o.-f.	+	.
<i>Cardamine flexuosa</i>	o.	o.	+	+	.
<i>Carex sylvatica</i>	+	f.-o.	o.	f.	r.
<i>Chrysosplenium oppositifolium</i>	l.f.	l.c.	r.r.	+	.
<i>Circaea lutetiana</i> (damper places)	o.	f. l.c.	f.c.	+	r.
<i>Cirsium palustre</i>	o.	l.f.	o.	+	.
<i>C. vulgare</i>	o.	o.	o.	.	.
<i>Clinopodium vulgare</i>	f.	o.-f.	f.-ab.	+	.
<i>Conopodium majus</i>	+	+	+	f.	r.-r.r.
<i>Deschampsia caespitosa</i> (flushes)	l.	l.-o.	r.r.-l.f.	f.	.
<i>Digitalis purpurea</i>	c.-f.	f.c.-c.	r.-o.	f.	.
<i>Dryopteris filix-mas</i>	o.	o.	o.	f.	r.r.-v.r.
<i>Epilobium montanum</i>	f.-l.c.	o.-f.c.	f.	+	o.
<i>Euphorbia amygdaloides</i>	f.-c.	f.-o.	l.ab.	f.-l.c.	r.r.-l.f.
<i>Festuca gigantea</i> (margin)	l.f.	r.	o.-r.	.	.
<i>Filipendula ulmaria</i> (flushes)	.	l.f.c.	l.f.	l.f.	.
<i>Fragaria vesca</i>	f.	f.-ab.	c.-l.ab.	f.-c.	r.r.
<i>Galeobdolon luteum</i>	f.	f.c.-c.	f.-c.	f.	r.r.-f.
<i>Galium aparine</i>	o.	+	+	+	.
<i>Geranium robertianum</i>	f.-f.c.	f.	f.	f.	.
<i>Geum urbanum</i>	f.	+	f.	+	r.r.
<i>Glechoma hederacea</i>	c.-l.ab.	o.	o.-f.c.	l.f.	o.-l.ab.
<i>Holcus lanatus</i>	l.ab.	f.c.	f.c.	+	.
<i>H. mollis</i>	c.-f.	ab.-c.	f.-c.	l.ab.	c.-r.
<i>Hypericum perforatum</i>	o.-f.	r.-l.c.	f.	o.	.
<i>Luzula pilosa</i>	o.-l.f.	c.	r.r.	f.-c.	o.-f.
<i>Lysimachia nemorum</i>	f.	f.-c.	o.-c.	f.	.
<i>Melica uniflora</i>	f.	f.	f.c.	f.c.-f.	.
<i>Mercurialis perennis</i>	c.-l.ab.	l.c.	ab.-c.	c.-ab.	l.ab.-r.r.
<i>Milium effusum</i>	.	r.	l.f.-r.	r.r.	.
<i>Oxalis acetosella</i>	c.	v.c.-c.	o.	f.-v.c.	o.-f.
<i>Poa nemoralis</i> (margin)	c.	c.	f.-f.c.	f.c.-v.c.	.
<i>Potentilla sterilis</i>	+	f.-f.c.	f.	o.	.
<i>Primula vulgaris</i>	o.	o.-c.	f.c.-c.	f.-v.c.	.
<i>Prunella vulgaris</i>	+	f.	c.	f.c.	.
<i>Pteridium aquilinum</i>	l.c.-ab.	l.ab.-f.	r.-c.	o.-r.	v.c.-l.ab.
<i>Ranunculus auricomus</i>	.	f.	o.-f.	l.f.	l.r.
<i>R. ficaria</i>	c.	l.c.-f.c.	l.ab.	l.c.	.
<i>R. repens</i>	r.r.-f.	l.f.	+	f.	.
<i>Sanicula europaea</i>	l.r.	l.	f.c.-ab.	c.	r.r.-f.
<i>Scilla non-scripta</i>	r.r.-c.	c.-l.ab.	f.-c.	f.-l.c.	r.r.
<i>Sorophularia nodosa</i>	o.	o.	o.	o.	r.r.

Arum maculatum

Table 1 (continued)

(a) Oakwoods (continued)

Field layer	...	1	2	3	4	5
<i>Tamus communis</i>		o.-v.r.	o.	f.-c.	r.r.	.
<i>Teucrium scorodonia</i> (margin)		f.-v.c.	f.c.-c.	c.	f.c.-c.	o.-f.
<i>Urtica dioica</i>		f.	+	o.	.	.
<i>Veronica chamaedrys</i>		f.	f.-c.	c.	f.	.
<i>V. montana</i>		+	l.f.	f.	+	r.r.
<i>V. officinalis</i>		l.f.	c.	o.	+	.
<i>Viola reichenbachiana</i>		+	o.	v.c.	v.c.	r.-o.
<i>V. riviniana</i>		+	o.-c.	v.c.	v.c.	r.-f.

(1) Beech woodlands of the South Downs (Watt, 1924, 1925).

(2) A beechwood on chalk, Ditcham Park, Hampshire (Adamson, 1921).

(a) Wolver Wood Series. Soil reaction pH 8.

(b) The Miscombe Series. Soil reaction pH 8.5.

(c) Oakham Bottom. A calcicolous coppice. Soil reaction pH 7.

(3) A beechwood of the Central Cotswolds on Inferior Oolite (Tansley & Adamson, 1913).

It is present in the ground vegetation in which there is no generally dominant species.

(b) Beechwoods

Field layer	1	2(a)	2(b)	2(c)	3
<i>Arum maculatum</i>	o.-l.f.	o.	o.	o.	o.
<i>Ajuga reptans</i>	o.-l.ab.	o.	o.-l.ab.	f.	r.
<i>Arctium minus</i>	o.	o.	o.	.	f.
<i>Arenaria trinervia</i>	r.-l.f.	.	o.	.	o.
<i>Asperula odorata</i>	l.ab.	f.	l.ab.	f.	ab.
<i>Brachypodium sylvaticum</i>	o.-f.	r.	l.	o.	ab.
<i>Carex sylvatica</i>	o.	.	l.	.	f.
<i>Chamaenerion angustifolium</i>	o.-l.d.	l.a.	.	l.ab.	o.
<i>Circaea lutetiana</i>	o.-l.ab.	l.	l.ab.	o.	l.ab.
<i>Cirsium palustre</i>	r.-l.ab.	.	.	r.	o.
<i>C. vulgare</i>	l.-r.	.	.	o.	.
<i>Clinopodium vulgare</i>	o.	.	.	o.-f.	.
<i>Epilobium montanum</i>	o.-l.ab.	.	o.	o.	f.
<i>Euphorbia amygdaloides</i>	o.-f.	l.f.	l.f.	o.	f.
<i>Fragaria vesca</i>	o.-l.ab.	l.f.	l.	ab.	ab.
<i>Galeobdolon luteum</i>	l.f.-l.ab.	l.f.	l.ab.	f.	o.
<i>Geranium robertianum</i>	o.-f.-l.ab.	.	r.	o.	f.
<i>Geum urbanum</i>	o.-f.	.	r.-o.	o.	o.
<i>Glechoma hederacea</i>	o.-l.ab.
<i>Melica uniflora</i>	o.	.	l.	.	ab.
<i>Mercurialis perennis</i>	o.-l.d.	o.-l.d.	l.d.	l.d.	l.ab.
<i>Myosotis arvensis</i>	o.	.	r.	l.	o.
<i>Primula vulgaris</i>	o.-f.	.	l.f.-l.ab.	o.	o.
<i>Prunella vulgaris</i>	o.-l.ab.
<i>Pteridium aquilinum</i>	o.-l.ab.	.	l.	.	l.ab.
<i>Ranunculus ficaria</i>	r.	.	l.ab.	.	.
<i>Sanicula europaea</i>	r.-l.f.	ab.	o.-l.ab.	ab.-f.	ab.
<i>Scilla non-scripta</i>	l.f.-l.ab.	.	l.ab.	.	l.ab.
<i>Scrophularia nodosa</i>	l.	.	o.	o.	.
<i>Urtica dioica</i>	o.-l.d.	.	o.	.	.
<i>Veronica chamaedrys</i>	o.-f.	o.	o.	o.	f.
<i>V. officinalis</i>	r.-l.ab.	.	r.	.	f.

(c) Composition of communities in beechwoods. On the Continent of Europe it is an important constituent of the field layer of beechwoods. It is present in the beechwood associates of many countries within its continental area of distribution. It is found with *Hepatica triloba*, *Ranunculus lanuginosus*, *Actaea spicata*, *Cardamine silvatica*, *Sanicula europaea*, *Asperula odorata*, *Lysimachia nemorum*, *Vinca minor*, *Veronica montana*, *Asarum europaeum*, *Neottia nidus-avis*, *Cephalanthera* spp., *Epipactis microphylla*, *Orchis purpurea*, *Cypripedium calceolus*, *Melica uniflora*, *Hordeum europaeum* (Lebensg. 1, iii, p. 34). In the beechwoods of Britain it has an equally important status (Table 1).

In a fox covert of 'mixed' trees on chalky boulder clay in north Lincs *Arum maculatum* is associated with other marginal species, *Viola odorata*, *V. riviniana*, *Geranium robertianum*, *Bryonia dioica*, *Anthriscus sylvestris*, *Torilis anthriscus*, *Chaerophyllum temulum*, *Lapsana communis*, *Glecoma hederacea* and *Stachys sylvatica* (Woodruffe-Peacock, 1918). The author says these plants were probably not on the site when the covert was planted, but have reached it by following the field fences abutting on to the wood. In a *Fraxinus* coppice in Rutland on oolitic limestone *Arum maculatum* grows in large clumps with *Mercurialis perennis* through a deep covering mat of *Porotrichum alopecurum*.

In hedgerows of *Crataegus monogyna* in Leicestershire it occurs with the following herbaceous plants: *Ranunculus auricomus*, *R. ficaria*, *Alliaria petiolata*, *Melandrium dioicum*, *Stellaria media*, *Arenaria trinervia*, *Geum urbanum*, *Anthriscus sylvestris*, *Hedera helix*, *Galium aparine*, *Lamium album*, *Mercurialis perennis* and *Urtica dioica*. In an orchard to which it has spread from an adjoining woodland in north Lancashire, it grows in the shade of the fruit trees with *Ranunculus ficaria*, *Viola riviniana*, *Myrrhis odorata*, *Primula vulgaris*, *Glecoma hederacea*, *Mercurialis perennis*, *Urtica dioica* and *Galanthus nivalis*.

IV. *Response to biotic factors.* Protected from grazing by the raphides contained in the leaves, although on the Continent leaves have been found in the stomach of the Common Crane (*Grus grus grus* (L.)) (Jourdain, 1940). It was observed in a Leicestershire wood in April 1946 that a large number of spathes had been bitten off at the base. Some of them were afterwards found on the branches of trees, and the damage can therefore probably be attributed to birds. This may be analogous to the destruction of other spring flowers such as the primrose and crocus by birds, or they may be torn off by birds seeking the slugs and snails which enter the spathe for shelter. It was noticed that this only occurred to plants growing in the wood; plants growing under hedgerows were untouched.

Whilst coppicing has the effect of reducing the organic content of the surface layer and its correlated acidity, the increase in light intensity does not appear to have a detrimental effect on the plant. After clear felling, however, the plants are scorched and depauperate in the following season. If regeneration is quick the plant will be saved from extinction. The examination of an area of woodlands which was clear-felled (Adamson, 1921) showed that *Arum maculatum* retained its frequency three years later, a flora of tall herbs 3-5 ft. in height providing the shade.

V. (a) *Gregariousness.* (b) *Performance in various habitats.* Generally grows in 'clumps' or patches of irregular shape. Some clumps show great variation of individual plants, whilst others show similarity. Clumps showing great similarity are probably due to cloning. This has been investigated by C. T. Prime who dug up and mapped the corms of a uniform colony. The direction of the growth of the corms was compatible with asexual reproduction from the original plants. Measurements of leaves of plants growing in clones show less variation in size than the leaves of plants chosen at random.

(c) *Effect of frost, drought, etc.* The young leaves are capable of withstanding frost in spite of their succulent nature. Leaves examined in a spinney in Leicestershire in the morning after a sharp frost were limp but were quite recovered three hours afterwards. The spathes are ruined by cold drying winds and do not unroll (Church, 1908). After the snowfall of 1 May 1945, many spathes were affected and failed to mature. They remained in a shrunken green condition and did not open (E. W. Jones).

VI. (a) *Morphology.* The slow-growing tuber is 2 cm. or more in diameter and contains

the food reserves accumulated during the summer. It is protected against underground animals by raphides. In autumn a leaf bud is developed for the next season's growth, and behind are one or more corms of the previous years on which there are ring-like leaf scars and root remains. The strongly contractile roots pull the tubers to a depth of 20–30 cm. from the surface. Scott & Sargent (1898) examined tubers which were 2 cm. below surface in May, and by October they were 7 cm. deep. Young tubers replanted near the surface will regain normal depth in a week.

(b) *Mycorrhiza*. Endotrophic mycorrhizal association of the arbuscular-vesicular type (Gallaud, 1915). Mycelium at first intracellular, later intercellular is the usual course of events, but the first condition may be quite evanescent (M. C. Rayner).

(c) *Perennation*. Stem tuber geophyte. Thick unbranched roots are found on the tuber by September, and then there is a cessation of all growth during the winter. By the end of July the leaves and spathes have withered and only the fleshy axis remains. This dies down after the dispersal of the berries or is killed by the frost, and those berries which are not eaten decay on the surface of the soil. Thus nothing is visible above ground during the winter. Daughter tubers are frequent and are budded off from the under-surface of the mature tuber. The plant produced from seed rarely flowers before the seventh year, whilst plants from daughter tubers flower much younger. Seed is set every year. C. T. Prime made counts of the number of ovules ripening in the fruits of the two forms of this species, and the percentage of ripe seeds of the spotted plants was 39.4, whilst of the unspotted plants was 37.6. The average number of ovules per gynaecium was 2.83 and 3.34 respectively.

(d) *Chromosome number*. The basic number is $n=14$. The following values of $2n$ have been reported: $2n=28$, Danish material (Hagerup, 1942, in Löve & Löve, *Scandinavian Flora*); $2n=32$, north German material (Schmucker, 1925) (? error for 28); $2n=56$, British material, near Leeds (H. G. Baker, 1946); $2n=56$, British and German material (*Mert. Cat.* 1939); $2n=84$, British material (*Mert. Cat.* 1940). Maude says this variation can probably be accounted for by polyploidy within the species.

(e) *Physiological data*. No information.

VII. *Phenology*. Each spring roots are developed below the leaf bud when the period of maximum growth commences. The leaf bud for the next season's growth is well developed by the autumn, and its base thickens out to form the tuber which will be initiated in the following spring. The leaves expand and uncoil from February to March or earlier in mild winters, e.g. in 1881, at Chelmsford, 26 December, and in 1882 at Saffron Walden, 1 January. The leaves and spathes are coiled 'sinistrally' or 'dextrally', and according to Christy (1914) the leaves on any one plant are always coiled the same way as the flower spathe of that plant. This was further studied and confirmed by Armitage (1921), who also found that there were hardly ever more 'dextrally' coiled than 'sinistrally' coiled spathes, i.e. five 'lefts' to four 'rights'. In the south of Britain it flowers early in April, becoming later in more northerly stations. In Wiltshire, Preston (1888) gives the first flowering 29 March 1882 to 13 May 1879. Average date, 22 April. The flowers are over by the middle of June, and the leaves have mostly gone by the end of July.

VIII. (a) *Floral biology*. Pollination is effected by midges of the genus *Psychoda* which are attracted to the flowers by the emission of an odour variously described as 'ammoniacal', 'urinous', 'disagreeable', 'foetid', etc. The colour of the spadix is considered also to be a further attraction to the midges. Dung flies have been observed to alight on the spadix, but they do not enter the spathe. There is a rise in temperature of the tip of the spadix

which Church (1908) records as 10–12° C. above the air temperature. The temperature in the floral chamber also rises 1–3° C. above the air temperature, and according to Dutrochet (in Balfour, 1871) the maximum temperature is reached at about 17.30 hr. The starch in the spadix is used up during this active metabolism, and the spadix then becomes limp. The midges enter the chamber through the ring of stiff bristles, which allows them to enter but prevents them from flying out until they have pollinated the female flowers with the foreign pollen which they have carried in on their bodies. The stigmas are receptive on the first day of opening. After pollination the stigmas shrivel and a drop of nectar is exuded. The anthers dehisce and shed pollen on the imprisoned flies up to the 3 days afterwards. The ring of bristles then shrivels and allows the insects to escape. It has often been observed that if a spathe is cut open the imprisoned midges immediately fly to another plant (Knuth, *Poll.* 3). Owing to the large number of midges found dead in spathes, it was suggested by the earlier botanists that the plant is insectivorous, but there is no evidence to support this (Arcangeli, 1883).

There is a suggestion that these dead flies have been suffocated by CO₂ from the respiring spadix. The number of midges found in spathes varies considerably and up to 4000 has been recorded (*Lebensg.* 1, 33–45). *Psychoda phalaenoides* L. is the species most commonly cited by writers. Tonnoir (1940) examined the insects found in spathes in various parts of Britain (Herts, Surrey, Sussex, Devon) and the total number of specimens of *Psychoda* determined were as follows: *P. phalaenoides* L., 0 ♂, 158 ♀; *P. grisea* Tonn., 14 ♂, 19 ♀; *P. trinodulosa* Tonn., 0 ♂, 2 ♀; *P. brevicornis* Tonn., 1 ♂, 2 ♀; *P. setigera* Tonn., 0 ♂, 1 ♀; *P. severini* Tonn., 0 ♂, 1 ♀. From these results he suspected *P. phalaenoides* to be parthenogenetic. Further investigations have been made, however, by G. H. Satchell (1944) of the midges in spathes collected over two years near Leeds. His records showed that *P. phalaenoides* was by far the most numerous visitor with 205 ♀ in all and *P. grisea* second with 38 ♀ and 2 ♂. *P. phalaenoides* was collected from tree trunks near the *Arum* plants at the same time, and both sexes were taken. The females taken from the *Arum* spathes were cultured and gave rise to both male and female offspring. It seems, therefore, that *Arum* is attractive to the female fly only. Other insects such as small beetles, weevils, and aphids are often found in the spathes with slugs, spiders and earwigs, but these stray visitors are probably merely seeking shelter and warmth.

(b) *Hybrids*. Colgan (1911) studied the ‘unspotted’ and ‘spotted’ forms of *A. maculatum* and suggested that the male parent was heterozygous for ‘spotted’ character and was fertilized by the ‘unspotted’ form, but there was no evidence in support beyond the equal proportion of the two forms among the offspring. It has been shown by Schmucker that self-fertilization and parthenogenesis do not occur, and this has been confirmed by the writer who blocked numbers of spathes with cotton-wool and found that no seeds were set. C. T. Prime also ‘bagged’ plants, and out of 47 plants, only one set seed. He also blocked the spathes of two plants and no seed was set. Crosses were also made by him of the extreme forms, and there did not seem to be any failures. Plants of *A. neglectum* (Townsend) Ridley (*A. italicum* auct. angl.) with spotted leaves are considered by Ridley (1938) to be hybrids with *A. maculatum*. The problem is being investigated by H. G. Baker (1947), whose accumulated evidence so far suggests that *A. maculatum* and *A. italicum* hybridize in this country.

(c) *Seed production and dispersal*. Frequency distribution of the number of fruit on 82 plants examined from Hertfordshire, Kent and Pembrokeshire gave 24.28 ± 0.34 .

Examination of 175 fruits showed a range in the number of seeds: 1(150), 2(16), 3(6), 4(3). 86% contained only one seed. The average seed output is 29.4 ± 1.1 seeds per plant (cf. Fig. 28, p. 176 and Table 89, p. 177, Salisb. *Rep. Capac.*). Colgan (1911) examined 661 ripe fruits and found an average of 1.4 seeds per fruit. Average seed weight in grams = 0.04536 (Guppy, 1912).

Seed dispersal. Ripe berries fall off the spadices or are dispersed by birds. Chaffinches (*Fringilla coelebs gengleri* Kleinschmidt) were observed to eat the berries (Scott & Sargent, 1898). Hulme (1902) says the seeds are eaten by many birds, including pheasants and others.

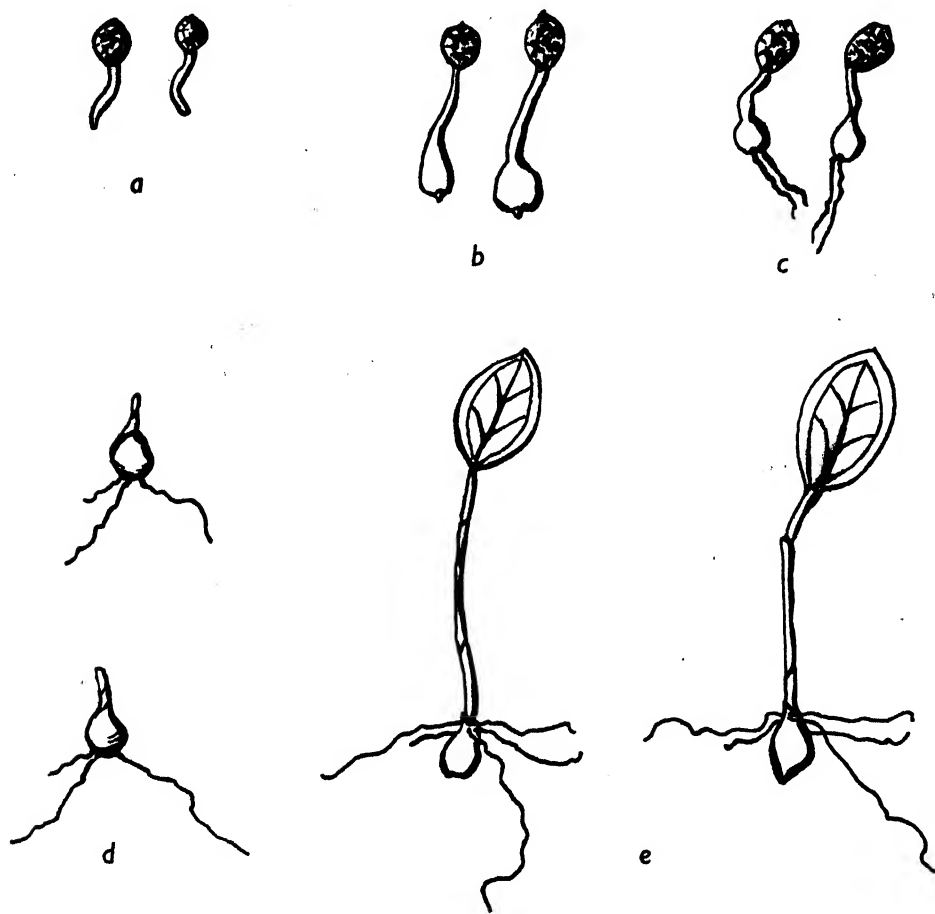


Fig. 2. *Arum maculatum* L. a-c, stages of germination: a, 9 days, the cotyledon has emerged from the seed coat; b, 23 days, the tuber has been formed by the thickening of the hypocotyl; c, 44 days, contractile roots have appeared. All grown on filter paper. $\times \frac{2}{3}$. d, seedling at the end of the second year. The stem bud is exposed. Grown in soil in pots. $\times \frac{2}{3}$. e, third year, the first (ovate) leaf. Grown in soil in pots. $\times \frac{2}{3}$.

(d) *Viability of seeds and special conditions affecting germination.* Sets of seeds were kept in Petri dishes at room temperature in daylight and in darkness. Germination in daylight, nil. Germination in the dark, 20%. Sets of seeds taken from 'unspotted' and 'spotted' leaved plants were planted in soil in pots out of doors and were examined for germination in the second year. The soil was frozen during the first winter. The following results were recorded: 'spotted' seed 85.71% germination, 'unspotted' seed 91.66% germination

(Sowter, 1945). The result of a germination test made by Salisbury (*Rep. Capac.* p. 177) was under 6%. Wattam (1938) planted 40 seeds in pots in the spring, and the contents of the pots were frozen during the winter. Germination was 100%.

(e) *Seedling morphology.* In Britain, as on the Continent, the seeds germinate in the early spring. First the seed swells and the cotyledon emerges from the seed coat (Fig. 2*a*). Then the hypocotyl thickens out to form the tuber from which grow two or three contractile roots (Fig. 2*b,c*). In the second season the seed coat is detached and the stem bud is exposed (Fig. 2*d*). According to Scott & Sargant (1898) no chlorophyll is formed and nothing is seen above ground. In the germination experiments made by the writer in soil, a large percentage of the seedlings showed a green leaf tip just above soil level. New roots (4-6) are sent out during the summer. As a rule it is not until the third year (Fig. 2*e*) that the first leaf appears above the surface, although Irmisch (1850) and Colgan (1911) report the first leaf in the autumn of the second year as an exception. The first leaf is ovate. Below ground the tuber increases in size until June, when next year's tuber is initiated. The tuber is pulled deeper in the ground each season by the contractile roots which are produced at the end of the summer. It also moves its position from vertical to horizontal. In the fourth or fifth year the first hastate leaf is formed, and flowering rarely occurs before the seventh year.

(f) *Effective reproduction.* Examination of clumps suggests that reproduction by vegetative means is more important than multiplication by seed. In addition to having a ready-made supply of foodstuff the tubers start at their normal depth in the ground and the risk of being eaten is therefore almost eliminated.

IX. (a) *Animal feeders or parasites.* Several thrips have been taken but are considered to be casual visitors probably not feeding (G. D. Morrison). No Cecidomyiids are known to be associated with it (H. F. Barnes). The oil beetle (*Meloe proscarabacus*) sometimes feeds on this plant (Briggs, 1880).

(b) *Plant parasites.* The alga *Phyllosiphon arisari* Kühn (Siphonales) which is occasionally parasitic on the leaves in Italy and the south of France (West & Fritsch, 1927) has been found on plants in Scotland at Tillietudlem Castle near Lanark. It causes yellow spots on the leaves (J. Caldwell).

The following fungi are recorded:

BASIDIOMYCETES

UREDINALES: *Caeoma ari-italici* (Req.) Rud., near Salisbury, 1897 (*Br. Rust. F.* p. 388); also found in France and Germany. *Puccinia phalaridis* Plowr. *Aecida* on *Arum maculatum* May-July (*Br. Rust. F.* p. 269).

FUNGI IMPERFECTI

HYPHOMYCETES: *Macrosporium ignobile* Karst Ayrshire, A. L. Smith & Ramsbottom, 1913 (*Trans. Brit. Mycol. Soc.* 4, 183); *Ramularia ari* Fautr. at Chipping Campden (*List Hyphomyc.* p. 94).

COELOMYCETES: *Ascochyta ari* Died. (Syn. *A. aricola* A. L. Smith & Ramsbottom) (*Br. Stem and Leaf F.* 1, 321).

X. *History.* There are no geological records.

XI. *General*. The starch obtained from the rhizomes has in the past been used for several purposes. In the Isle of Portland the starch extracted was sold as 'Portland Sago' (Henslow, 1905). In Elizabethan times it was used to starch the lawn ruffs worn during that period. In Switzerland the rhizomes have been used as a substitute for soap. Medicinally the action of a small dose of the powdered root is diaphoretic. Fatal effects have been recorded from large doses. Children have died from eating the berries. The toxic principle is believed to be saponin. Animals exceptionally eat the plant (Long, 1924). Observations made in Leicestershire near Badger 'setts' suggest that this animal grubs for the roots in winter. Pigs eat the roots (Cornevin, 1887). Gilbert White (1789) says the roots are scratched out from hedgebanks and eaten by birds in winter.

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NOTICES

PLEISTOCENE RESEARCH

In June 1947, the Division of Geology and Geography of the National Research Council set up a Committee on Interrelations of Pleistocene Research. The objectives of this Committee are: (1) to inventory research in progress; (2) to formulate problems which should be attacked, with particular reference to those involving two or more disciplines; (3) to provide for interchange of information between workers. A report on the findings of the Committee is in preparation. Its membership is as follows:

EDWARD S. DEEVEY, Jr., *Biogeography*.

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U.S. Department of Agriculture, Lincoln, Nebraska.

Probably no group so broadly representative of the various disciplines which find their common meeting ground in Pleistocene research has ever been set up. Certainly none has ever functioned efficiently in carrying out the above objectives. The co-operation of biologists in particular is solicited in this notice. Suggestions, references, reprints of pertinent papers, and information regarding research in progress, will be welcome from all interested scientists. Biological information should be sent to the undersigned, who conceives biogeography to include all biological data derived from existing distributions of animal and plant species from Pleistocene fossils (though much fossil material will be handled by members representing stratigraphy and vertebrate palaeontology), and from post-glacial stratigraphy, including pollen analysis. Matters of more general importance may be communicated to the Chairman.

EDWARD S. DEEVEY, Jr.

FOREST ECOLOGY IN INDIA

Dr G. S. Puri has been appointed Forest Ecologist at the Forest Research Institute, Dehra Dun, U.P., India, and would welcome assistance from ecologists, especially in the form of ecological literature concerning forest conditions. He will have the good wishes of the Society in his task of developing this most promising field of research.

STUDIES ON GROWTH AND DEVELOPMENT IN *LOLIUM*I. RELATION OF THE ANNUAL HABIT TO HEAD PRODUCTION
UNDER VARIOUS SYSTEMS OF CUTTING

BY J. P. COOPER

Welsh Plant Breeding Station, University College of Wales, Aberystwyth

AND S. W. SAEED*

*Hyderabad Government College, Pakistan**(With twelve Figures in the Text)*

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I. INTRODUCTION

A study of the comparative morphology and physiology of related ecological forms, either within one species or between closely related species, is of considerable interest, not only from the purely ecological standpoint, but also as indicating the lines along which evolutionary changes may have taken place. In the case of herbage plants, there is the added interest that the agronomic value, not only of different species, but also of types within a species, depends largely on their reaction to such environmental factors as light and temperature, in addition to the biotic factors of grazing, cutting and manurial treatments.

In view of the importance of such studies, investigations were begun on the comparative morphology and physiology of a related group of herbage grasses, namely, the outbreeding species of the genus *Lolium*. This group, which comprises three species, *L. rigidum* Gaud., *L. italicum* Braun and *L. perenne* Linn. (Jenkin & Thomas, 1938), shows a wide range of ecological and agronomic types, ranging from the early flowering annual *L. rigidum*, through the biennial *L. italicum*, to varying degrees of perenniality in *L. perenne*, which itself contains both early and late flowering forms. These three species are wind-pollinated, normally cross-fertilized and all are diploids with $2n=14$.

* The data from the cutting experiments were collected by S. W. Saeed and presented in part fulfilment of the requirements for the degree of M.Sc. of the University of Wales.

Although usually considered as three separate species, all are to a considerable extent interfertile, and produce viable and fertile hybrids in the F_1 and subsequent generations. The cross *L. italicum* \times *L. perenne* has been studied by Jenkin (1931*a*), who finds no evidence of incompatibility, nor of sterility, in the F_1 generation, and considers that these types must be regarded as fully interfertile. In the cross *L. rigidum* \times *L. perenne*, Jenkin & Thomas (1938) report 22% good pollen and dehiscent anthers in the F_1 hybrid. An inversion bridge is reported in a backcross of the F_1 to *L. perenne*, but such irregularities also occur within *L. perenne* itself (Myers, 1941). Results obtained by one of the present writers (S. W. S.) give a seed set of 70.3% for one cross of *L. perenne* \times *L. rigidum*, while the F_1 hybrids crossed gave mean seed sets of 12.1%. From these results *L. rigidum* and *L. perenne* may be regarded as comparatively interfertile, even if not completely so.

The wide range of types makes this group very suitable for comparative study, while, since all are interfertile, it should be possible to investigate the genetic basis of the morphological and physiological differences.

The present paper is concerned with the relation between the annual or perennial habit and head production under various intensities of cutting. One of the most noticeable effects of cutting lies in its influence on subsequent head production, as shown by a later ear emergence, a decreased number of heads and a decreased stem percentage in the herbage.

The importance of high seasonal productivity, combined with a quick recovery after cutting or grazing, has been stressed from the early days of grassland investigation, and the reaction of different herbage species has been studied extensively from the agronomic point of view (Stapledon, 1924; Graber, 1931). As a result of this early work, the general effects of cutting treatments on total productivity are well established, namely, that the greatest yield is obtained from the most lenient systems of cutting.

In the present work data are presented on the effect of various cutting treatments on head production, seasonal productivity under these treatments is analysed into its components, and an attempt is made to relate this behaviour to the growth form and annual or perennial habit of the types concerned.

II. MATERIAL AND METHODS

A. *Species and strains employed*

The range of ecological types within the group is represented by the following six populations grown from seed.

(1) *Lolium rigidum* Gaud. Wimmera ryegrass, provided by Prof. Trumble of the Waite Agricultural Research Institute, Adelaide. This species is an annual of Mediterranean origin, and is grown extensively in the Wheat Belt of Victoria as a grazing plant. Under British conditions it forms a semi-erect plant with many lax flowering stems. The flowering culms are long and slender, the spikelets inserted on the rachis as in *L. perenne*, and the outer glume is shorter than the spikelet. The florets are normally cross-pollinated, the anthers being fully exerted before dehiscence.

In the past, the term 'Wimmera ryegrass' has also been applied to another distinct species, *L. loliaceum* Hand-Maz. This is a small prostrate annual with very short stiff flowering shoots. The spikelets are closely appressed to the rachis and completely covered by a long stiff outer glume, so that the inflorescence has a cylindrical appearance. The

florets are normally self-pollinated, and little pollen is shed outside the paleae. The taxonomic and genetic differences between these two species have been studied by Jenkin & Thomas (1939), and it must be emphasized that the term 'Wimmera ryegrass' in the present paper refers only to the first species, *Lolium rigidum* Gaud.

(2) *Lolium italicum* Braun. Italian ryegrass from seed of commercial stocks grown in Northern Ireland. This species is normally a biennial, giving its greatest yield in the first harvest year and dying out in the next season. It possesses a rather erect and tufted growth habit, though the stems carry more leaf than in Wimmera. Tillering is not so pronounced as in *L. perenne*, and most new tillers are produced not at ground level but from aerial nodes. As a result the plant does not spread well over the surface of the ground, and is generally used as a hay rather than as a pasture plant.

(3) *Lolium perenne* Linn. Four distinct types of this species are studied, comprising one commercial and three bred strains. All types are less erect and more highly tillering than Italian or Wimmera, with a lower proportion of fertile tillers. As a result of this rapid tillering and comparatively low and dense growth, they quickly form a spreading turf and are used largely for grazing purposes.

(a) *Irish commercial ryegrass from seed of commercial stocks grown in Northern Ireland.* This is an early-flowering type, rather erect in growth habit and inclined to be stemmy. It produces a less dense sward than the more prostrate types and is also less persistent.

(b) *Aberystwyth S. 24 from stock seed.* This bred strain is early-flowering like Irish commercial, but has been selected on a basis of greater spring growth and better recovery after cutting. It is, in general, rather more leafy and persistent than Irish commercial.

(c) *Aberystwyth S. 23 from stock seed.* This strain is late-flowering and high-tillering, and being prostrate in habit forms a very dense sward. It is based on plant material from old grazed pastures and has been selected for persistency under heavy grazing conditions.

(d) *Aberystwyth S. 101 from stock seed.* This, like S. 23, is a late-flowering strain, originating from material from old pastures. It is slightly earlier in heading than S. 23, and rather more erect in habit. Though primarily a grazing strain its more erect habit and longer leaf give it possibilities as a hay plant.

It should be noted that all three bred strains have been deliberately selected for absence of flowering stems in the aftermath, and, associated with this, relative absence of flowering stems in the seeding year when sown in the spring.

The agronomic features of these bred strains have been discussed by Jenkin (1943). Although the term 'strain' is commonly used only for the pedigree selected types, in this paper each of the six lots will be referred to as a 'strain' for purposes of convenience.

B. Systems of cutting

Seeds of each sample were sown under glass in June 1946, and the seedlings transplanted to the field in September 1946 as spaced single plants. The experimental layout consisted of a randomized block, each strain being represented by four replicates of forty plants each. During autumn and winter 1946-7 observations were made on head production, if any, and winter survival. The first cutting treatments began on 16 April 1947, some 3 weeks after spring growth had started in the earlier strains.

Although the cutting treatments were used primarily to study their effect on head production, they correspond closely to those used by Stapledon (1924) for the evaluation

of seasonal productivity in various herbage species, and it is therefore possible to compare the present results with his experimental data. The treatments employed were:

- (1) A fortnightly pasture cut beginning 16 April, roughly simulating close grazing conditions;
- (2) A monthly pasture cut beginning 16 April, representing a more lenient system of grazing.

These two treatments were begun on 16 April, before ear emergence had occurred in any of the strains, and were carried out at the same dates for all strains, irrespective of their stage of maturity. In the next two treatments the cuts were based not on date as such, but on stage of development of the plants concerned.

- (3) Date of ear emergence cut for each plant, followed by a second cut when aftermath flowering had begun and subsequently by monthly cuts.

The standard of ear emergence used at the Welsh Plant Breeding Station is that date when the first three heads have just emerged from the leaf sheath. It represents a recognizable stage in the development of the plant (Jenkin, 1931*b*).

- (4) Date of flowering cut for each plant followed by a second cut when aftermath flowering had begun and subsequently by monthly cuts.

This corresponds to the 'hay and aftermath' cuts of Stapledon (1924). Flowering was taken as that date when anthesis had begun in the first three heads.

Except for the first emergence and flowering date cuts the unit of cutting was the row of ten plants, each replicate of forty plants being divided into four rows of ten, corresponding to the four cutting treatments.

All cuts were made at a uniform height of 1 in. from ground-level, and the cut herbage was immediately removed and weighed. For each cut, the number of heads emerged was recorded, together with the green weight per plant or per row. After weighing, the herbage from each row was bulked and a sample of about 1 lb. was air dried, being later separated into 'stem' and 'leaf'. In these studies 'stem' comprises both stem and leaf sheath, while 'leaf' applies to leaf blade only. All weights are given in ounces.

III. RESULTS

A. *Effect of cutting on head production*

The course of head production in the various strains under the different cutting systems will first be described, and then the effect of single cuts on heading will be analysed in relation to the developmental cycle of the plant.

Two criteria are used for head production: first, the number of heads emerged during the interval between cuts, and secondly, the 'stem' percentage in the cut herbage.

The curves for number of heads and 'stem' percentage under each cutting system are given in Figs. 1-8, and for tracing the course of head production under the different treatments either of the two criteria may be used.

(1) *Fortnightly pasture cuts beginning 16 April* (Figs. 1 and 5)

The first cut includes, in addition to spring growth of leaf, a certain proportion of elongated stem and/or leaf sheath from the preceding winter. The stem percentage of this first cut is highest in Wimmera, which contains many old flowering stems, and is lowest

in the late-flowering perennials which had not begun elongation by 16 April. The early-flowering S. 24 and Irish, and the biennial Italian form an intermediate group, some elongation having already started. In all strains, except Wimmera, there is a reduction in stem percentage in the second cut, due to the previous removal of stems or leaf sheaths from the winter, but as soon as elongation of new flowering shoots begins, the stem percentage increases, even before actual ear emergence.

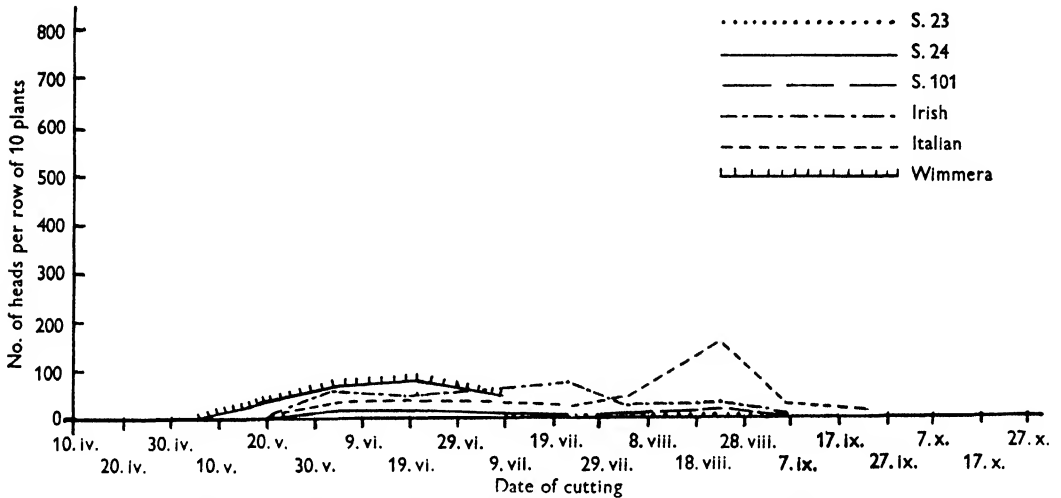


Fig. 1. Number of heads in strains of *Lolium*: fortnightly pasture cuts.

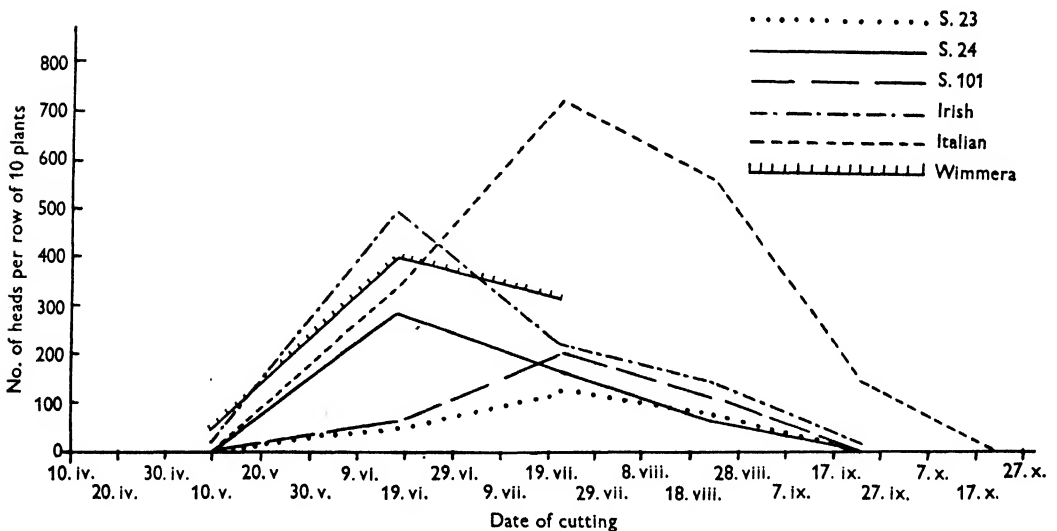


Fig. 2. Number of heads in strains of *Lolium*: monthly pasture cuts.

During this pre-emergence period, the strains are grouped according to earliness or lateness of ear emergence. The cut of 19 May, for instance, shows a great increase in stem percentage for the early-flowering strains (Wimmera, Irish and S. 24) where flowering stems have already begun to elongate, while in the intermediate (Italian) and late-flowering strains (S. 23 and S. 101) this increase does not occur till later (Fig. 5).

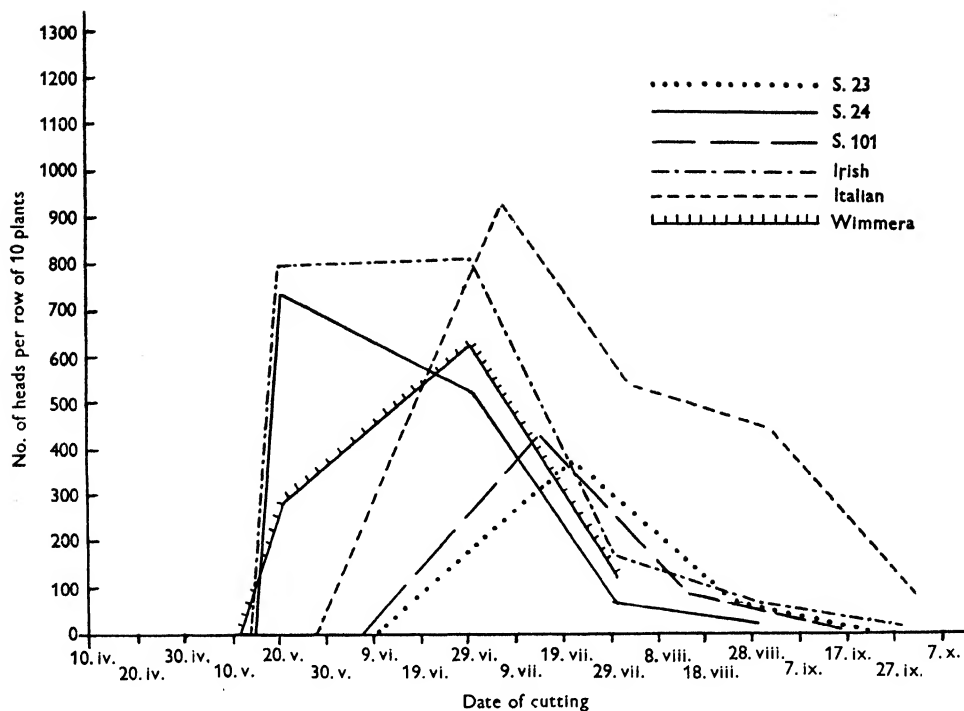


Fig. 3. Number of heads in strains of *Lolium*: date of emergence cut.

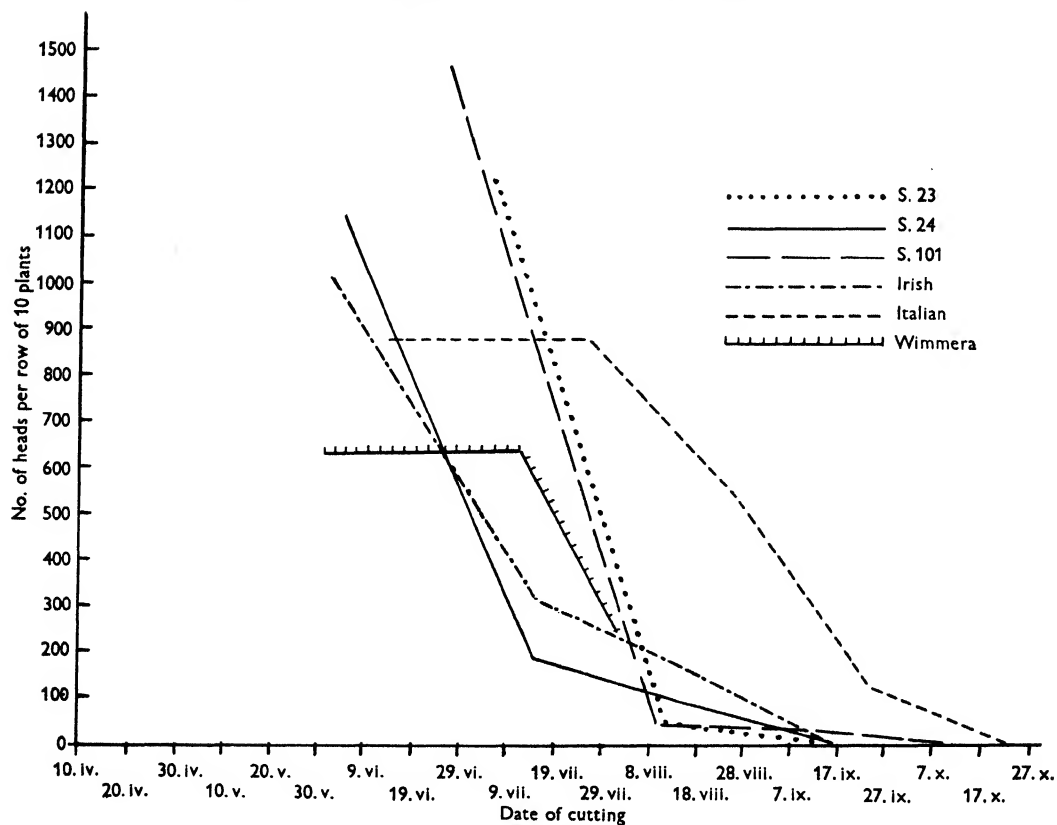


Fig. 4. Number of heads in strains of *Lolium*: date of flowering cut.

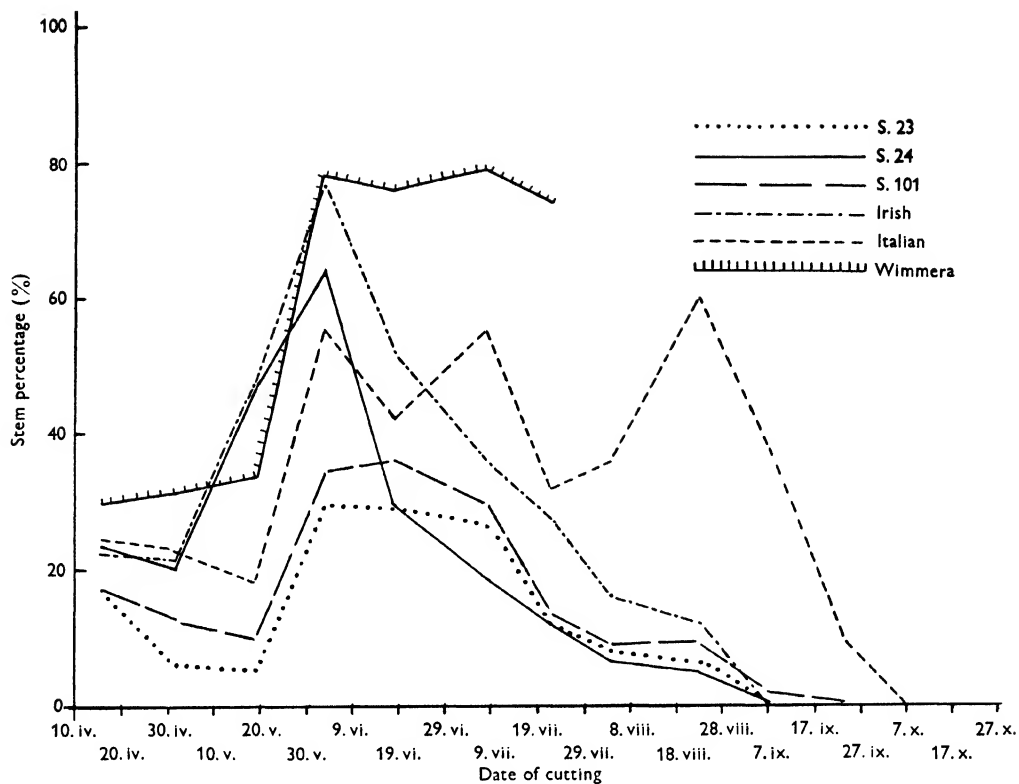


Fig. 5. Stem percentage in strains of *Lolium*: fortnightly pasture cuts.

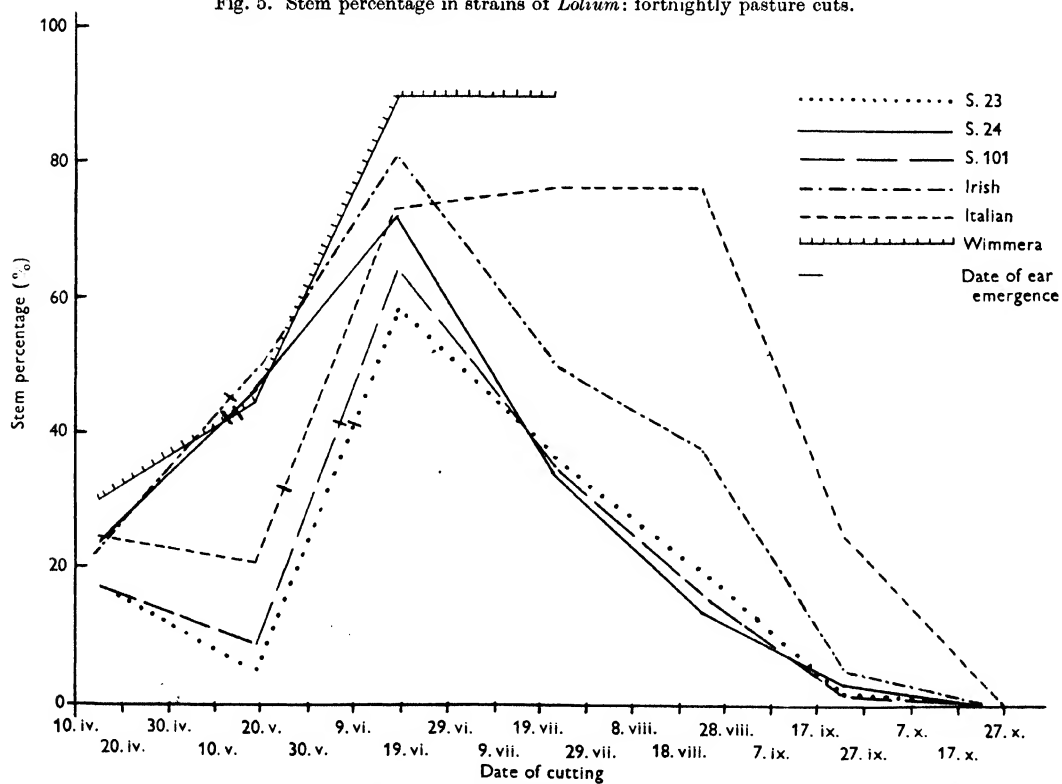


Fig. 6. Stem percentage in strains of *Lolium*: monthly pasture cuts.

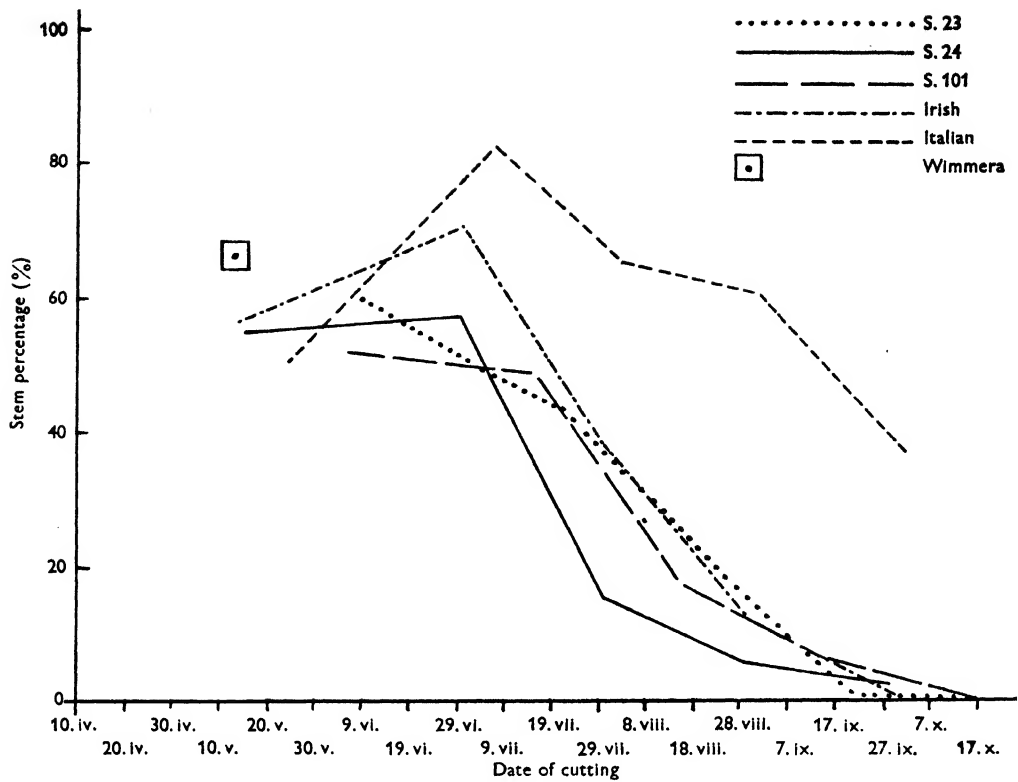


Fig. 7. Stem percentage in strains of *Lolium*: date of emergence cut.

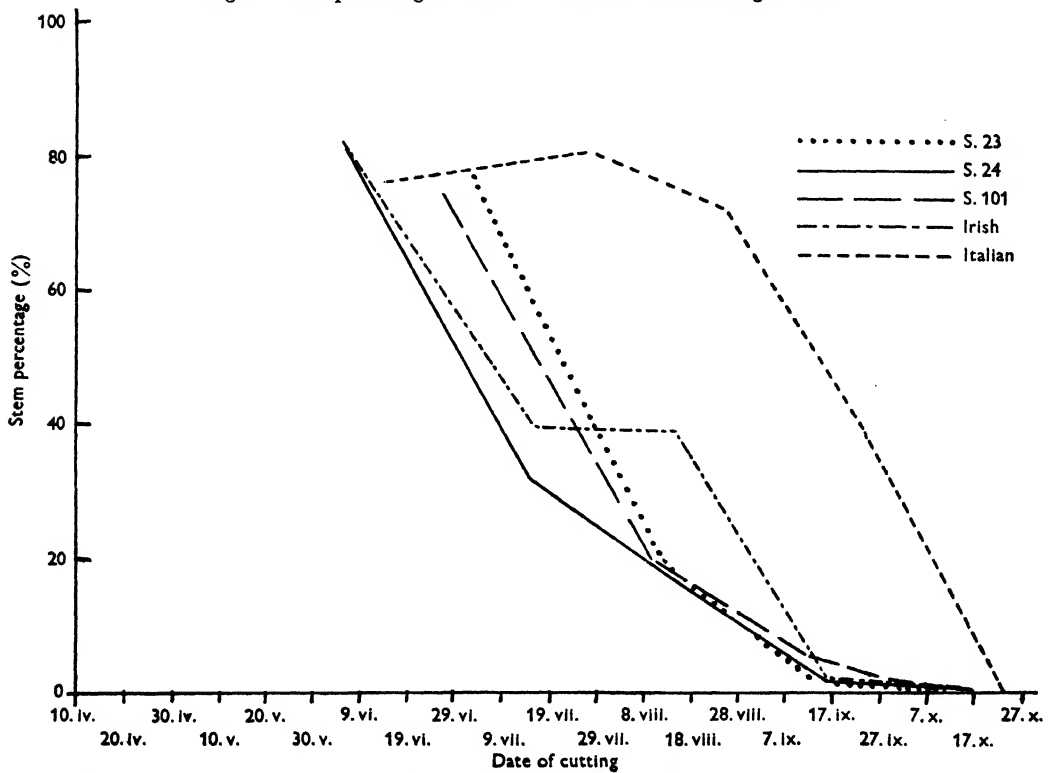


Fig. 8. Stem percentage in strains of *Lolium*: date of flowering cut.

After ear emergence a rather different grouping of the strains is noticeable, this time into annual or perennial types. In the bred strains (S. 24, S. 101 and S. 23) there is a steady decline in head production during the cuts following ear emergence. The curves for these three strains all follow the same course, although at the peak of flowering the early S. 24 produced far more heads than the two later strains. The annual and biennial strains (Wimmera and Italian) react quite differently. After the initial increase accompanying ear emergence, head production continues steadily throughout the summer, being brought to an end by death of the plants in Wimmera, and, presumably, by shortening of day length for Italian.

The fluctuations in stem percentage which are noticeable in Italian seem to be due to the differing intervals between cuts which were not always exactly 14 days apart. Parallel fluctuations can be seen on a minor scale in Wimmera, and even in the extreme perennials S. 23 and S. 101, but do not affect the general trend except in Italian. The 14-day interval of cutting seems to be just on the threshold for head production in Italian, small deviations in either direction greatly affecting heading, while 14 days is quite ample for Wimmera and far too short for S. 23 and S. 101.

Irish appears to be intermediate between the selected strains and the annual or biennial. The initial increase in stem percentage is similar to that for S. 24, but reaches a higher peak value, and its decrease in stem percentage and number of heads is much more gradual. From this point of view, Irish is a semi-perennial type.

(2) *Monthly pasture cuts beginning 16 April* (Figs. 2 and 6)

The same pattern of head production can be seen in the monthly cuts as in the fortnightly. With the decreased frequency of cutting, head production is less inhibited than in the fortnightly cuts. In Italian, the 14-day cutting interval came near to preventing heading, but heads appear regularly throughout the summer with a 28-day interval.

The graphs in Figs. 2 and 6 show very clearly the distinction between the initial period of stem elongation and the subsequent continuation of head production through the summer. The cut of 18 June forms a convenient dividing line between the two periods of growth. Before this date the curves fall into three groups corresponding to emergence date, i.e. early (Wimmera, Irish, S. 24), intermediate (Italian), and late (S. 101 and S. 23). With subsequent treatments annual-perennial grouping becomes apparent, Wimmera and Italian continue to produce heads through the summer, while the stem percentage of the selected strains rapidly decreases. Irish is again intermediate.

(3) *Date of ear emergence and subsequent cuts* (Figs. 3 and 7)

In this treatment all plants were cut at equivalent stages of development. The initial cuts show little difference in stem percentage between strains when all are cut on their dates of ear emergence, and, of course, the number of heads is the same for all at this date. In the second cut, made when aftermath flowering had begun, the number of heads had increased in all cases, but the increase is greatest for Wimmera and Italian and least for the selected strains (S. 24, S. 101 and S. 23). The stem percentage, in the second cut, while increasing considerably for the biennial Italian and also for Irish, remained stationary for the early-flowering S. 24, and actually decreased for the late-flowering S. 23 and S. 101. Unfortunately, no stem percentages are available for Wimmera under this and the following treatment.

In subsequent cuts the same trends are observed as in the monthly and fortnightly cuts, head production decreasing rapidly in the selected strains, while Italian continues heading till late autumn.

(4) *Date of flowering and subsequent cuts* (Figs. 4 and 8)

There is little difference between the stem percentages of the various strains at the flowering stage. There are, however, considerable differences in the number of heads, these being most numerous in the late-flowering strains (S. 101 and S. 23), and least in Italian and Wimmera. This means that although cutting treatments severely inhibit head production in the late-flowering strains, and therefore stem percentage tends to be low, when the plant is left undisturbed until its usual flowering time, it produces a far higher number of heads per plant than do the annual or biennial types.

After the initial cut, the curves for both stem percentage and number of heads are very similar to those of previous treatments. In the first aftermath cut there is a great decrease both in stem percentage and in number of heads for the selected strains and for Irish. In Italian the same number of heads is produced in the aftermath as in the initial cut, while the stem percentage actually increases.

To sum up, the course of head production under the different systems of cutting is evidently related to the annual or perennial habit of the strain concerned. In the annual Wimmera and biennial Italian, heading continues throughout the summer, even under a fortnightly cutting interval, and at the same time the production of new vegetative tillers is severely curtailed. In the bred strains, which may be regarded as extreme perennials, head production rapidly decreases after the initial peak at ear emergence, and new vegetative tillers are produced in profusion. The Irish commercial strain appears intermediate. In the selection of material for the bred strains considerable importance was attached to absence of heading in the seeding year, and in the aftermath of the first harvest year. The highly perennial nature of these strains is thus the result of deliberate selection by the breeder.

B. *Seasonal productivity in relation to heading*

So far only the effect of different cutting systems on the course of head production has been discussed. It is important, however, to consider what relation head production bears to seasonal productivity in the various strains, and particularly, to recovery after frequent cutting.

The course of seasonal productivity for the different strain-treatment combinations is shown in Figs. 9-12, and can be compared with the corresponding curves for head production. These productivity curves were constructed by bulking the weight of all forty plants in each cut and plotting the accumulated weight against time.

The general pattern of both total and seasonal productivity can be seen from the figures, but to estimate the significance of the differences analyses of variance were made, for total yield, and for the following seasonal components:

- (1) Winter and spring growth (from the initial pasture cuts).
- (2) Hay yield (from the initial flowering date cut).
- (3) Aftermath yield (from the second flowering date cut).
- (4) Recovery after frequent cutting (from the later pasture cuts).

These analyses are shown in Tables 1-5.

(1) *Fortnightly pasture cuts beginning 16 April (Fig. 9)*

The first pasture cut taken on 16 April is composed not only of fresh spring growth, but also of a certain amount of old autumn and winter herbage. The yield of herbage in the initial cuts is comparatively small. Figs. 9 and 10 show differences in initial yield between strains, and this is confirmed by the analysis of variance (Table 1). The early-starting Italian and S. 24 are more productive than the later S. 23 and S. 101, which had only just begun active growth, and Wimmera was the lowest of all.

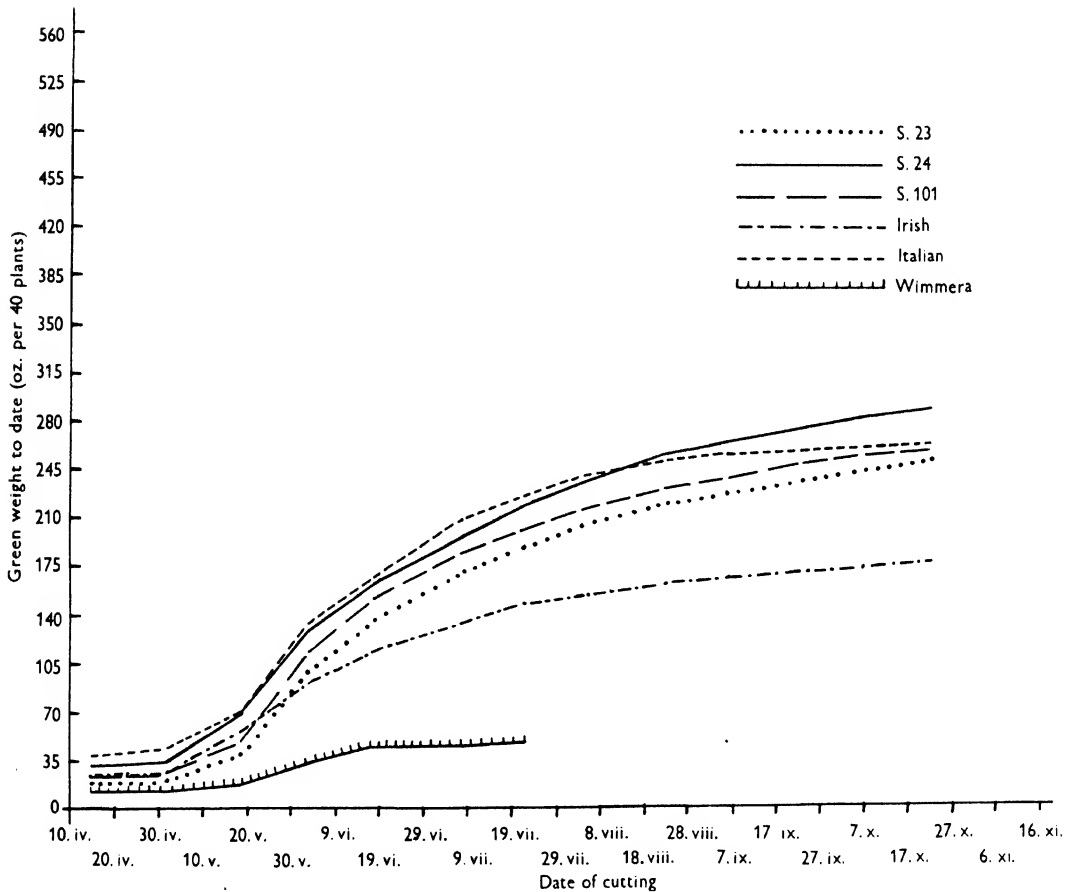


Fig. 9. Seasonal productivity in strains of *Lolium*: fortnightly pasture cuts.

There is little regrowth of leaf before the second cut, Italian and S. 24 appearing most active at this stage. From then onwards there is steadily increasing growth in all strains with a particularly sharp rise during the period 19 May to 3 June. After this initial rise, productivity gradually falls off as the season advances.

The curves for the three bred strains are remarkably parallel throughout the season, there being no significant difference in total yield between S. 23 and S. 101, and significance only at $P=0.05-0.01$ between S. 24 and S. 23. S. 24, although often regarded as a hay strain, behaves as well under pasture cuts as the pasture strains S. 23 and S. 101. Moreover, although S. 24 is early-flowering and S. 23 and S. 101 late-flowering, the curves

Table 1. *Winter and spring growth in strains of Lolium. Analysis of variance*

	Degrees of freedom	Sum of squares	Mean square	Variance ratio
Rows	1	0.8	0.8	0.19
Blocks	3	14.4	4.8	1.13
Strains	5	146.2	29.2	6.86***
Error	38	162.1	4.3	—
Total	47	323.5		

For $n_1=24$, $n_2=1$, variance ratio = 249.3 ($P=0.05$).

For $n_1=3$, $n_2=30$, variance ratio = 2.9 ($P=0.05$).

For $n_1=5$, $n_2=30$, variance ratio = 5.5 ($P=0.001$).

*** indicates significance at $P<0.001$.

Strain differences are significant at $P<0.001$; other differences are not significant.

Standard error of single plot mean = $\sqrt{(4.3)} = 2.07$.

Standard error of mean of 8 plots = $\sqrt{(4.3/8)} = 0.730$.

Comparison of strains: weight in oz. per row of ten plants						Standard error mean of 8
Italian	S. 24	Irish	S. 101	S. 23	Wimmera	
8.43	7.44	5.66	4.94	4.63	3.21	0.73
For significance at $P<0.05$,				difference must exceed 2.09.		
For significance at $P<0.01$,				difference must exceed 2.79.		
For significance at $P<0.001$,				difference must exceed 3.66.		

show no large differences in the period of maximum growth under pasture cuts. At the end of the season the bred strains were still showing appreciable recovery after each cut.

The annual, Wimmera, gives consistently lower yields in every instance. Once the emergence date is reached, every tiller rushes into head with a minimum of leaf production. As a result, by the end of July, most of the plants had become exhausted and died out, so after this date no further cuts were taken.

In Italian, although a biennial, gross productivity was high and equal to S. 24 throughout the early part of the season, surpassing it at midsummer. As cutting continued, recovery after each cut became less and less until its final yield was equal only to that of S. 101. In Irish, after an initial increase in weight comparable to that of Italian and of the selected strains, productivity rapidly falls off, and both total yield and recovery after cutting are much below the selected strains.

(2) *Monthly pasture cuts beginning 16 April* (Fig. 10)

The general picture is rather similar to that shown by fortnightly cutting. After the first cut a slow increase in productivity to 19 May is apparent, with S. 24 and Italian leading, and a sudden rise occurs over the period 19 May to 18 June. After this date the yields for each cut fall off, but the decrease is at first smaller for Italian than for the other strains. However, by the end of the season, the recovery of Italian is significantly lower than that of the selected strains, though its high summer productivity gives it a higher total yield.

The curves for the three selected strains are again parallel. Irish, while intermediate between the early-flowering S. 24 and later S. 23 and S. 101 for the first two cuts, rapidly tails off after that and gives a low total yield. Wimmera is again low throughout. In all strains the more lenient monthly cutting gives a higher total yield than does the fortnightly one.

Neither the fortnightly nor the monthly pasture cuts shows any sign of the 'secondary peak' of growth observed by Stapledon (1924) to coincide with the date of aftermath production as the 'primary peak' corresponded to ear emergence.

(3) *Date of ear emergence and subsequent cuts* (Fig. 11)

In this and the following treatment the plants were cut at comparable stages of development, and hence not on the same date for all strains.

From this treatment a modification of the results of the monthly cutting is obtained. The highest productivity is given by Italian with a high yield at the initial cut and a greater productivity in the first aftermath cut, but there is a tailing-off as cutting continues and recovery is markedly less than in the bred strains. The three selected strains again show parallel productivity even though S. 24 is early flowering and S. 23 and S. 101 are late, and therefore the date of the initial cut varies. Irish produces only slightly less than does S. 24 at the initial cut, but its total yield is lower than all except Wimmera.

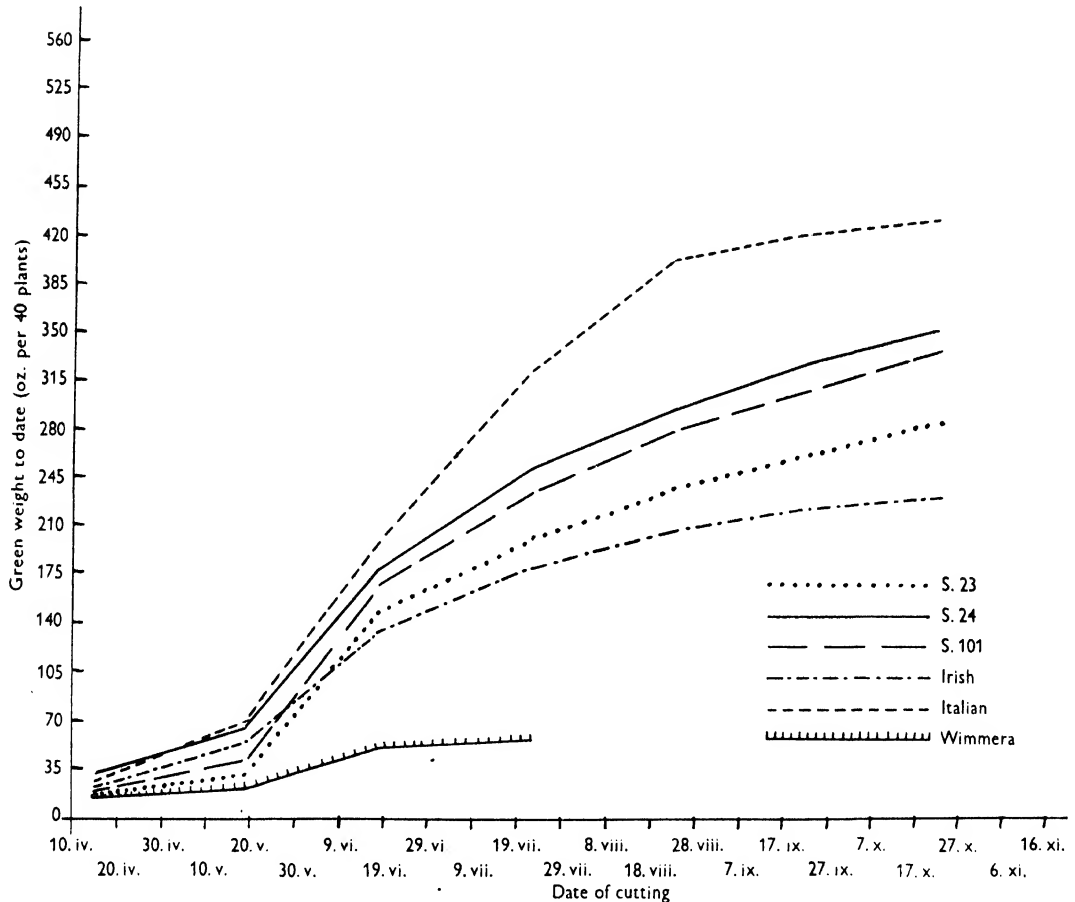
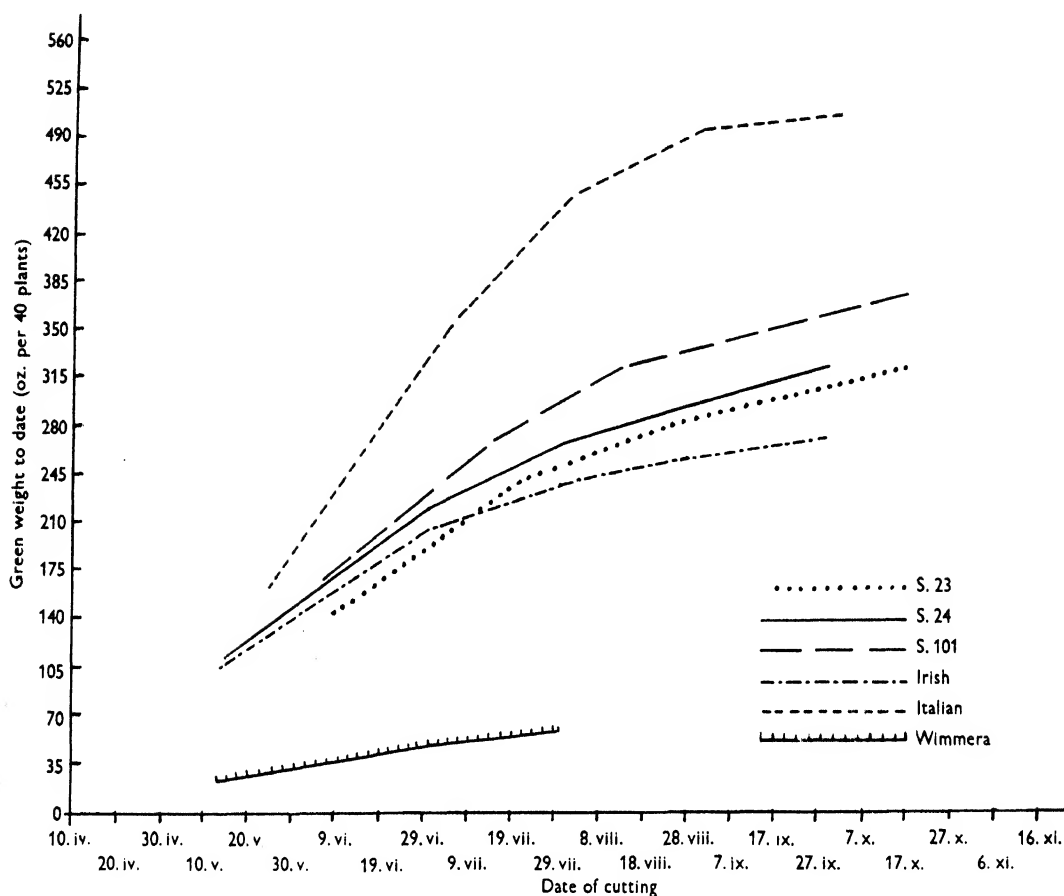


Fig. 10. Seasonal productivity in strains of *Lolium*: monthly pasture cuts.

(4) *Date of flowering and subsequent cuts* (Fig. 12)

This cutting system represents the usual hay and aftermath cuts of farming practice, a great part of the weight of the initial cut being made up of flowering culms. Since the strains were all cut at the same stage of development, the later flowering types were allowed a longer time for vegetative growth.

In spite of this difference in duration of growth, the analysis of variance for the initial

Fig. 11. Seasonal productivity in strains of *Lolium*: date of ear emergence and subsequent cuts.Table 2. Yield from flowering date cut in strains of *Lolium*. Analysis of variance

	Degrees of freedom	Sum of squares	Mean square	Variance ratio
Blocks	3	257.0	85.7	0.97
Strains	5	9,921.0	1,984.2	22.47***
Error	15	1,325.0	88.3	
Total	23	11,503.0		

For $n_1=15$, $n_2=3$, variance ratio = 8.74 ($P=0.05$).

For $n_1=5$, $n_2=15$, variance ratio = 9.34 ($P=0.001$).

*** indicates significance at $P<0.001$.

Strain differences are significant at $P<0.001$; block differences are not significant.

Standard error of single plot mean = $\sqrt{(88.3)} = 9.40$.

Standard error of mean of 4 plots = $\sqrt{(88.3/4)} = 4.70$.

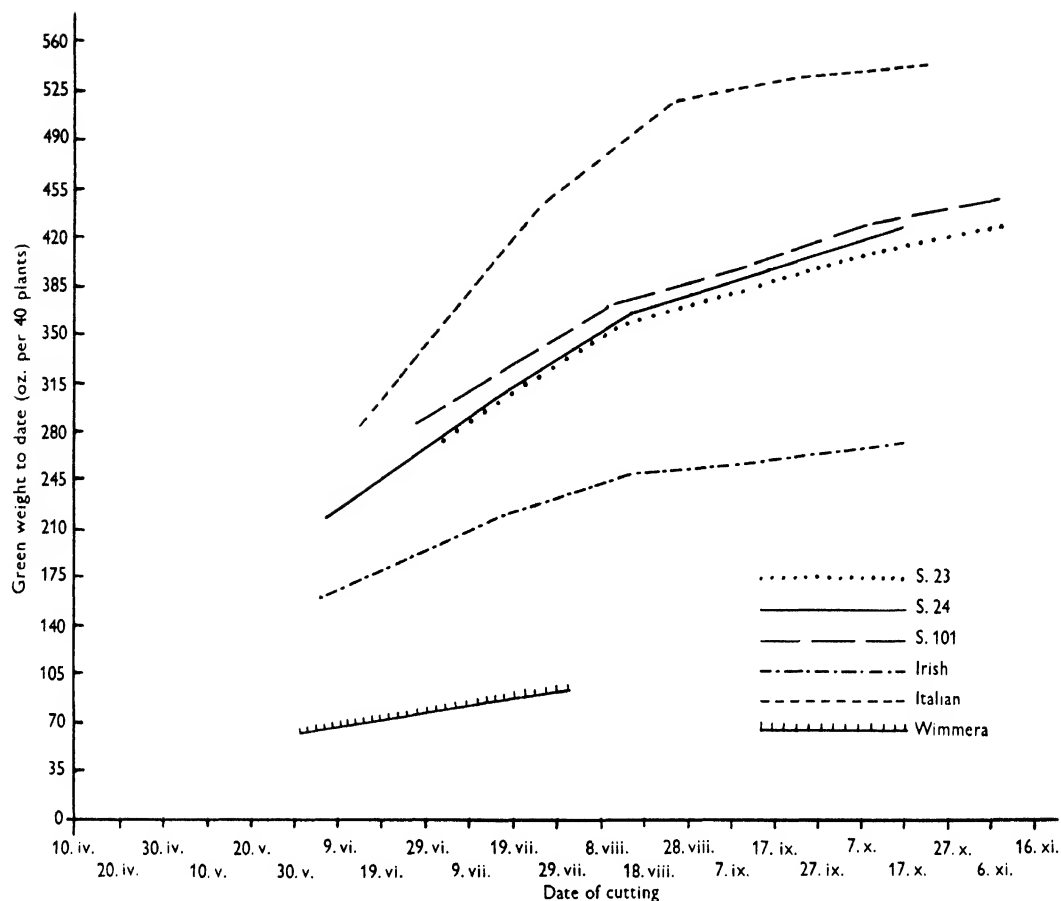
Comparison of strains: weight in oz. per row of ten plants

S. 101	Italian	S. 23	S. 24	Irish	Wimmera	Standard error mean of 4
71.26	70.62	68.24	54.35	40.26	15.07	4.70

For significance at $P<0.05$, difference must exceed 14.7.

For significance at $P<0.01$, difference must exceed 18.28.

For significance at $P<0.001$, difference must exceed 27.08.

Fig. 12. Seasonal productivity in strains of *Lolium*: date of flowering and subsequent cuts.Table 3. Yield from first aftermath cut in strains of *Lolium*. Analysis of variance

	Degrees of freedom	Sum of squares	Mean square	Variance ratio
Blocks	3	8.0	2.7	0.26
Strains	5	2766.0	553.2	53.19***
Error	15	156.0	10.4	—
Total	23	2930.0		

For $n_1=15$, $n_2=3$, variance ratio = 8.74 ($P=0.05$).

For $n_1=5$, $n_2=15$, variance ratio = 9.34 ($P=0.001$).

*** indicates significance at $P<0.001$.

Strain differences are significant at $P<0.001$; block differences are not significant.

Standard error of single plot mean = $\sqrt{(10.4)} = 3.22$.

Standard error of mean of 4 plots = $\sqrt{(10.4/4)} = 1.61$.

Comparison of strains: weight in oz. per row of ten plants

	S. 24	S. 101	S. 23	Irish	Wimmera	Standard error mean of 4
Italian 40.67	22.04	21.00	20.85	13.67	5.18	1.61

For significance at $P<0.05$, difference must exceed 4.86.

For significance at $P<0.01$, difference must exceed 6.27.

For significance at $P<0.001$, difference must exceed 9.28.

hay cut (Table 4) shows no significant difference between the late-flowering S. 23 and S. 101, and the intermediate Italian (the three highest yielders), while the difference between these and the next, S. 24, is significant only at $P=0.05-0.01$. Irish is significantly less than S. 24, with Wimmera far below.

In the aftermath cut, taken when the secondary heads were in flower, the biennial Italian has a much greater yield than any of the others, largely because of a greater number of heads (Table 3). There are no significant differences between the bred strains, but Irish is significantly below these three in spite of possessing a greater number of heads. Wimmera is very poor indeed.

When hay, aftermath and subsequent cuts are considered, Italian gives the highest total yield, although its initial hay weight is no higher than S. 101 or S. 23. But although the increase in the aftermath cut is much greater in Italian, its recovery after cutting declines towards the end of the season (Table 4). In this, the most lenient cutting, the recovery of Italian is still less than that of the selected strains and of Irish. The selected strains again show parallel productivity with no significant differences in aftermath or in

Table 4. *Recovery after cutting in strains of Lolium. Analysis of variance*

	Degrees of freedom	Sum of squares	Mean square	Variance ratio
Blocks	3	3.2	1.07	1.88
Strains	4	170.1	42.52	74.58***
Treatments	2	57.5	28.75	50.44***
Interaction	8	13.0	1.63	2.86*
Error	42	23.7	0.57	—
Total	59	267.5		

For $n_1=3$, $n_2=40$, variance ratio = 2.84 ($P=0.05$).

For $n_1=4$, $n_2=40$, variance ratio = 5.70 ($P=0.001$).

For $n_1=2$, $n_2=40$, variance ratio = 8.25 ($P=0.001$).

For $n_1=8$, $n_2=40$, variance ratio = 2.18 ($P=0.05$),
= 2.99 ($P=0.01$).

*** indicates significance at $P<0.001$.

* indicates significance at $P<0.05$.

Both strain and treatment differences are significant at $P<0.001$.

Strain-treatment interaction is significant at $P=0.05-0.01$.

Block differences are not significant.

Standard error of single plot mean = $\sqrt{(0.57)} = 0.755$.

Standard error of mean of 12 plots = $\sqrt{(0.57/12)} = 0.226$.

Standard error of mean of 20 plots = $\sqrt{(0.57/20)} = 0.169$.

Comparison of strains: weight in oz. per row of ten plants

S. 24	S. 101	S. 23	Irish	Italian	Standard error mean of 12
5.84	5.51	5.09	2.60	1.67	0.226

For significance at $P<0.05$, difference must exceed 0.646.

For significance at $P<0.01$, difference must exceed 0.864.

For significance at $P<0.001$, difference must exceed 1.134.

Comparison of treatments: weight in oz. per row of ten plants

Flowering date	Monthly	Fortnightly	Standard error mean of 20
4.85	4.82	2.76	0.169

For significance at $P<0.05$, difference must exceed 0.483.

For significance at $P<0.01$, difference must exceed 0.646.

For significance at $P<0.001$, difference must exceed 0.847.

total yield (Table 5). Irish gives significantly lower yields than all except Wimmera, in hay, in first aftermath and in total yield.

(5) *Recovery after frequent cutting*

One of the most valuable agronomic properties of a herbage plant is its ability to recover rapidly after frequent cutting or grazing.

Recovery after cutting for each treatment was measured by the fresh weight increase from 23 September to 23 October, that is, by the last cut in the monthly treatments, and the sum of the last two in the fortnightly cuttings. For recovery after the date of flowering and subsequent cuts, interpolation from the production curve was employed for the same range of dates. The behaviour of the strains is shown graphically in Figs. 9, 10 and 12, while the analysis of variance is given in Table 4.

Data were analysed from the fortnightly and monthly pasture cuts, and also from the date of flowering and subsequent monthly cuts, to see whether any carry-over of depletion of reserves occurred between one monthly cut and the next.

There is no significant difference between the bred strains (S. 24, S. 101, S. 23) in capacity for recovery. Irish is significantly lower than these and Italian less still. This is in distinct contrast to the high total productivity of Italian, but what would be expected from its known agronomic behaviour as a short-lived hay plant. The Wimmera shows little or no recovery, even after the cut of 22 July, so on the standard of measurement adopted here its recuperative capacity is zero.

In all strains recovery under monthly cuts was significantly greater than under fortnightly, the latter not providing sufficient time for replacement of reserves in the roots and stubble. There is, however, no significant difference between recovery after monthly pasture cuts throughout the season, and recovery after the flowering date cut followed by monthly cuts. Apparently a monthly interval between cuts provides sufficient time for re-storage of reserves to take place and there is no carry-over of depletion from one month to the next.

In the annual Wimmera and biennial Italian several cases occurred of the extreme situation—no recovery at all—the plants having died out, this happening more frequently in Wimmera (Table 6).

The association between high recovery and low head production is very noticeable. The annual and biennial strains with continued head production through the summer are those very forms which die out most readily under frequent cutting, while the bred strains with a high recuperative capacity show a rapid decrease in heading after the initial peak. This association between recuperative capacity and low head production after cutting is evidently an expression of the annual or perennial habit.

(6) *General conclusions*

For the initial cuts in all treatments, Italian is superior, but as cutting continues, its capacity for recovery declines and with the most frequent cuttings this brings its total yield below some of the selected strains. From the analysis of variance of total yield combining all treatments (Table 5) Italian gives the highest total fresh weight. The strain treatment interaction is, however, significant at $P=0.05-0.01$. An examination of the data shows this to be due mainly to the differential response of Italian to continued cutting.

The bred strains show parallel curves of productivity under all treatments, with similar

Table 5. *Total yield for season in strains of Lolium. Analysis of variance*

	Degrees of freedom	Sum of squares	Mean square	Variance ratio
Blocks	3	875.0	291.7	1.61
Strains	5	83,677.0	16,735.4	92.17***
Treatments	3	18,916.7	6,305.6	34.72***
Interaction	15	6,603.0	440.2	2.42**
Error	69	12,529.0	181.6	—
Total	95	122,600.7		

For $n_1=3$, $n_2=60$, variance ratio $=6.17$ ($P=0.001$).

$$= 2.79 \text{ } (P = 0.05).$$

For $n_1=5$, $n_2=60$, variance ratio = 4.76 ($P=0.001$).

For $n_1=12$, $n_2=60$, variance ratio = 3.31 ($P=0.001$).

$$= 2.50 \quad (P = 0.01).$$
$$= 1.92 \text{ } (P = 0.05).$$

*** indicates significance of $P < 0.001$.

** indicates significance of $P < 0.01$.

Strain differences and treatment differences are significant at $P < 0.001$.

Strain-treatment interaction at $P=0.05-0.01$.

Standard error of single plot mean = $\sqrt{(181.6)} = 13.47$.

Standard error of mean of 16 plots = $\sqrt{(181.6/16)} = 3.37$.

Standard error of mean of 24 plots = $\sqrt{(181.6/24)} = 2.75$.

Comparison of strains: weight in oz. per row of ten plants

Comparison of strains, weight in oz. per row of ten plants						Standard error
Italian	S. 101	S. 24	S. 23	Irish	Wimmera	mean of 16
108.73	88.83	86.71	80.45	59.70	15.74	3.37

For significance at $P < 0.05$, difference must exceed 9.53.

For significance at $P < 0.01$, difference must exceed 12.68.

For significance at $P < 0.001$, difference must exceed 16.47.

Comparison of treatments: weight in oz. per row of ten plants

Fortnightly	Monthly	Emergence date	Flowering date	Standard error mean of 24
53.32	70.24	77.53	92.18	2.75

For significance at $P < 0.05$, difference must exceed 7.78.

For significance at $P<0.05$, difference must exceed 7.78.
For significance at $P<0.01$, difference must exceed 10.35.

For significance at $P<0.01$, difference must exceed 10.50.
For significance at $P<0.001$, difference must exceed 13.46.

Table 6. *Survival after cutting in annual and biennial strains of Lolium*

The figures represent the number of plants surviving out of forty originally planted in the block.

[illegible]

recuperative capacity, in spite of the difference in ear emergence and flowering date between the early S. 24 and the later S. 23 and S. 101; S. 23 is slightly less productive throughout than the other two.

Irish starts active growth in the spring before the late S. 23 and S. 101, but under all treatments, productivity decreases after the second cut and total yield is low in every case, significantly below all the bred strains.

The annual Wimmera gives a low yield for all treatments, its herbage being composed largely of heads and it has a very small recuperative capacity.

When the strain results are combined, the analysis of variance (Table 5) indicates highly significant differences between the effects of the various systems of cutting. The highest total yield in all cases is obtained from the most lenient cutting—the date of flowering and subsequent cuts—while yield decreases as intensity of cutting increases.

These figures for total and seasonal yield confirm the results obtained by many workers (Stapledon, 1924; Weinmann, 1948) that frequent cutting diminishes the total green weight production and that different species and strains vary in their response to different cutting treatments. In the present work, however, an attempt is made to relate these differences in yield to the annual or perennial habit and developmental cycle of the strains concerned.

IV. DISCUSSION

The majority of experiments involving cutting treatments and the varying responses of different strains or species have been carried out from the purely agronomic point of view to determine the effect of strain or treatment on total yield. The literature on this subject is rather extensive and has been reviewed by Graber (1931) and Weinmann (1948).

In this work two main aspects of the problem have been studied; first, the effect of cutting on head production in relation to the annual or perennial habit; and secondly, seasonal productivity and recovery after cutting in relation to storage and depletion of food reserves.

A. *The annual habit and head production after cutting*

It has been found by many workers that cutting in the herbage grasses both delays the initial emergence of heads and also decreases their total number. Stapledon (1924), working on several species, including *L. perenne*, found that as the frequency of cutting increased, the stem percentage decreased, the exact effect depending on the date at which cutting was started. Repeated cuts decreased stem more than leaf at all dates, different species and strains varying in the extent to which heading was diminished. The results of the present work in general confirm these observations.

To understand the effect of cutting on head production it is necessary first to examine the course of inflorescence development in the undisturbed plant. The course of primordium differentiation in *Lolium*, and its relation to temperature and photoperiod, is being studied in detail by one of the present writers (J. P. C.) and will form the subject of a separate paper. Here only such aspects will be mentioned as bear on the reaction to cutting treatments.

The development of the inflorescence in *Lolium* follows the same general plan as in other members of the Gramineae (Purvis, 1934; Sharman, 1947). The vegetative shoot apex consists of a cylindrical meristem, blunt in *L. perenne*, elongated in *L. italicum* and *L. rigidum*, giving rise to leaf primordia, which eventually elongate and ensheath it.

Under the influence of suitable external conditions of temperature and photoperiod, the shoot apex elongates, the leaf primordia themselves are suppressed, but their axillary buds develop into spikelet buds. These spikelet buds later form the spikelets of the typical *Lolium* head. Under field conditions, this differentiation of spikelets is followed by elongation of the flowering stem and emergence of the ear.

Table 7. *Effect of sowing date on subsequent ear emergence in strains of Lolium out of forty originally planted in the block*

Sowing date	Irish		S. 24		S. 23	
	No. plants heading out of forty	Mean ear emergence 1947	No. plants heading out of forty	Mean ear emergence 1947	No. plants heading out of forty	Mean ear emergence 1947
22 Mar. 1946	40	18 May	40	18 May	40	13 June
2 Nov. 1946	40	12 May	40	14 May	40	22 June
20 Jan. 1947	38	4 June	36	22 June	31	21 July
21 Feb. 1947	27	31 July	23	8 Aug.	0	—
20 Mar. 1947	13	14 Aug.	13	5 Aug.	0	—

In no plants of *L. perenne* and *L. italicum* examined have differentiated flowering shoots been found during the winter, even when flowering had occurred in the previous season. Throughout the winter the shoot apex remains in the vegetative condition and it is not until March and April that spikelet buds can be detected. The particular date at which differentiation begins varies from strain to strain, and is noticeably affected by spring temperature. High spring temperature causes earlier spikelet differentiation, at least in the early-flowering strains, S. 24 and Irish. This earlier development of spikelet buds is followed by a correspondingly earlier date of ear emergence. In spring 1947 microdissection showed spikelet buds to be produced about the beginning of April in S. 24 and Irish, with mean ear emergence on 15 May. For the late-flowering S. 23, spikelet buds were formed in early May with mean ear emergence on 9 June.

The above observations apply only to plants overwintered in the field. When the various strains are sown in spring or early summer, considerable differences are noted in their ability to produce heads in the summer or autumn of that same year. In the present experiment all strains were sown together in July, but autumn heading occurred only in the annual Wimmera and biennial Italian. Table 7 shows the reaction of Irish, S. 24 and S. 23 to a series of sowing dates during winter and spring 1946-7. In all strains later sowing decreases the number of plants in each lot which produce heads in the same year, and also delays the date of ear emergence. In the late-flowering S. 23, sowing after the end of January completely prevented head formation that same season. Microdissection showed that this failure of heading was due to lack of spikelet differentiation rather than to prevention of stem elongation. Although all strains were exposed to the same long day and high temperature of summer, not all could respond to these conditions and form heads.

This situation seems to correspond closely to that investigated by Purvis & Gregory (1937) in spring and winter rye. They found that development of the inflorescence was influenced by external conditions of photoperiod, but before the stem apex could respond to these conditions it must have become 'ripe to flower'. This ripeness to flower is indicated morphologically by the production of a certain minimum number of leaves. In their work on spring rye they found that the first seven primordia always produced leaves, no matter what the external conditions, but the eighth to the twenty-fifth were labile and could

give rise to either leaves or spikelet buds. The effect of spring conditions is to switch development of these labile primordia from leaf to spikelet production. In unvernallized winter rye, the minimum leaf number was much higher, about twenty-five, although this could be reduced by suitable low-temperature germination.

The observations on autumn heading in *Lolium* suggest that the various strains do not become 'ripe to flower' with equal rapidity. With a July sowing some plants of the annual Wimmera and biennial Italian seem to reach this condition very quickly, but the Irish and the bred strains do not become 'ripe to flower' before the short days of autumn.

Observations by one of the present authors (J. P. C.) on the various strains grown in continuous light at 50–60° F. show that under these conditions Wimmera and Italian ryegrass are 'ripe to flower' after a minimum leaf number of 8–12, while in Irish and S. 24 this is higher (> 20). The same Wimmera and Italian lots, when sown in autumn and overwintered outside, produced 14–15 leaves before spikelet differentiation in the spring.

Spikelet formation and elongation of heads has been induced in overwintered Italian, S. 24 and S. 23 plants by treatment with continuous light in January (A. R. Beddows, unpublished). These results imply that by early spring many of the shoots of an overwintered ryegrass plant are already 'ripe to flower'.

As far as the cutting treatments are concerned, two main points of importance emerge: first, the greater rapidity with which the annual Wimmera and biennial Italian become 'ripe to flower', and secondly, the differing dates in the spring on which spikelet development begins in the various strains.

The initial divergence in stem percentage on the basis of ear emergence is a result of the different dates at which spikelet development and head elongation begin. By early spring all the strains have become 'ripe to flower' and spikelet differentiation can be induced by suitable temperature and photoperiod. When a cut is taken after head elongation has begun, those stem apices which were 'ripe to flower' will have produced spikelets and elongated, and so will be removed.

Table 8. *Effect of emergence date or flowering date cuts on head production in strains of Lolium*

(Figures represent number of plants producing heads after a single cut on the date indicated out of forty originally planted in the block.)

Strain	Emergence date cut	No. of plants heading	Flowering date cut	No. of plants heading
Italian	25 May	40	14 June	40
Wimmera	13 May	40	31 May	40
Irish	14 May	40	5 June	39
S. 24	15 May	40	6 June	35
S. 101	6 June	40	27 June	22
S. 23	9 June	30	3 July	20

After this cut only the young apices of the side-tillers remain. In the annual and biennial these become 'ripe to flower' very rapidly, and will have developed heads before the next cut. Head production may thus continue throughout the season. A fortnightly cutting interval is just on the threshold for head production in Italian, although quite ample for Wimmera. In the perennial strains, the young shoots take longer to become 'ripe to flower' and consequently few heads are produced even with a monthly cutting interval.

As the date of cutting becomes later, a critical date will be reached, differing from strain to strain, when the young apices remaining after cutting will be unable to reach the

minimum leaf number before the decreasing day length of autumn inhibits spikelet differentiation.

Table 8 shows the effect of a single cut, either at the emergence date or at the flowering date, on subsequent heading. Only in S. 23 does a single cut on the date of emergence prevent subsequent heading, and then only in ten out of forty plants. A single date of flowering cut, however, prevents further head production in some plants of all the perennial strains, though not in Wimmera or in Italian.

Table 9. *Head production in primary and secondary tillers of Wimmera ryegrass*

(All sown 16 November 1948 and grown in continuous light at 50–60° F.)

Main tiller		Secondary tillers					
		First tiller		Second tiller		Third tiller	
Leaf no.	No. of days from germination to ear emergence	Leaf no.	No. of days from tiller appearing to ear emergence	Leaf no.	No. of days from tiller appearing to ear emergence	Leaf no.	No. of days from tiller appearing to ear emergence
8	68	4	38	4	42	3	39
8	71	4	41	5	47	4	36
9	88	6	65	5	57	5	38
10	88	5	46	5	41	4	24
11	91	6	58	5	50	5	34
12	88	4	58	5	50	4	48

In the perennial strains the 'critical date' of cutting may be as early as the first flowering date for some plants, while in the annual and biennial it is much later, in early autumn. Consequently, in the later part of the season, the typical annual-perennial grouping is noticeable, the annual and biennial continuing to produce heads, while the perennials cease doing so. It is the earliness of this 'critical date' of cutting in the bred strains which is responsible for their rapid decrease in head production after the initial peak of ear emergence, and this early 'critical date' itself depends on the longer time required for these strains to become 'ripe to flower'.

In this discussion it has been assumed that the effect of cutting on head production is due simply to the mechanical removal of elongated stem apices. Many workers have shown that the perception of photoperiod takes place initially in the leaves (Lang & Melchers, 1943), and removal of the leaves by cutting may interfere with this process.

It is also important to know whether the different tillers of a plant are autonomous in becoming 'ripe to flower', or whether one main shoot can influence its axillary tillers. In plants of S. 24 sown in the spring, although 6 weeks elapse between the appearance of the main shoot and the first axillary tiller, the two produce heads within a few days of each other. Again in Wimmera the axillary shoots often produce heads after only the prophyll has been formed. Table 9 shows the dates of ear emergence and leaf numbers of the first four tillers in Wimmera seedlings grown in continuous light at 50–60° F. In all cases, the minimum leaf number of secondary tillers shows a decrease compared to the main shoot, while the days to ear emergence show a corresponding decrease. These results indicate that the tillers of one plant are not autonomous, the main shoot being able to affect the 'ripeness to flower' of its axillary buds.

The fact that it is the annual and biennial strains which so quickly become 'ripe to flower' raises the question as to what is an 'annual' and what a 'perennial' in the ryegrasses. In one sense, each individual tiller is an annual, since it possesses only determinate growth.

It can produce only one flowering spike and then die. The terms 'annual' and 'perennial' as commonly employed, refer only to the colony of tillers forming one single plant. If production of new tillers from axillary buds exceeds the death of the old ones after flowering, as in the extreme perennial S. 23, the plant as a whole will survive. If the older shoots rapidly elongate and form heads with little or no new tillering from the axils, as in the annual Wimmera, the plant will gradually diminish in size and finally die.

The annual or perennial habit seems to be due to some physiologic balance between, at the one extreme, rapid initiation and elongation of the flowering shoot with little proliferation of axillary buds, and, at the other extreme, profuse development of axillary buds as tillers with comparatively slow differentiation of the inflorescence. Data on *L. perenne* seedlings obtained by one of us (J. P. C.) suggest that heading is accompanied by a marked decrease in the rate of tiller production which until then was exponential (Cooper, 1948). Plants of the early-flowering S. 24, when kept in 9 hr. daylength are prevented from heading: tillering is much more pronounced than in the controls, and the plants assume a dense and prostrate habit of growth.

A decrease in tillering associated with head elongation has been noted in wheat by Bakhuysen (1947), who reports that auxin in block agar could be substituted for the elongating spike with the same effect. This decrease in tillering he attributes to 'correlative bud inhibition', active auxin production by the terminal spike inhibiting the development of the axillary buds.

Apart from this, the same axillary buds, which in the vegetative condition would have produced tillers, during head formation give rise to spikelets. Hence a rapid differentiation of the flowering shoot, with its accompanying low number of leaves, will automatically limit the number of axillary buds from which tillers can arise, and thus lessen the rate of tiller production.

To sum up, the different response to cutting in annuals and perennials appears to be due to the different lengths of time taken by the stem apex to become 'ripe to flower', that is, capable of spikelet differentiation under suitable conditions of temperature and photoperiod. In all strains, cutting removes elongating flowering shoots. In the annual Wimmera and biennial Italian the remaining stem apices become 'ripe to flower' very quickly, elongate and produce heads before the next cut. For Wimmera, an interval of 14 days is sufficient for spikelet differentiation and heading. In Italian, 14 days is slightly too short for complete elongation, although 20 days is quite sufficient. In the perennial strains, after removal of the flowering shoots, the remainder become 'ripe to flower' much more slowly, and with midsummer cuts may not attain that condition before the short days of autumn make conditions unsuitable for spikelet differentiation.

B. *The annual habit and seasonal productivity*

It has been generally observed in herbage species that frequent cutting decreases both shoot and root production, the decrease in production being proportional to the intensity of defoliation. In general, only work which deals directly with the ryegrasses will be considered here.

Stapledon (1924) found in various species, including *L. perenne*, that hay and aftermath cuts greatly exceeded pasture cuts in gross yield, and that cutting to ground-level severely reduced the yield as compared to a 2-in. cut. Roberts & Hunt (1936) studied the effect of cutting treatments on the root and shoot growth of perennial ryegrass. With a 10-day

interval recovery was very low, and all plants were killed out during the first year. Lengthening the cutting interval to 30 days extended the productive period and increased the total yield. An interval of 10 days was apparently too short to allow re-storage of reserves to the original level, while 30 days is quite sufficient. The lower the level of cutting the less was the recovery, since the smaller was the amount of photosynthetic tissue remaining after cutting. Roberts & Hunt also found a considerable decrease in dry weight of the roots during head elongation, while the total plant dry weight remained constant. They suggest that during vegetative growth reserve material is stored in the roots, being drawn upon by the flowering shoot during elongation. Jacques (1937), working with *L. perenne* and *L. italicum*, observed two main types of root, 'white roots' which were thick, glossy and straight and covered with root hairs, and 'fibrous roots' which were thin and wavy, and quickly became lignified. The 'white roots' are very quickly affected by defoliation, both in number and size, and it is suggested that they contain stored carbohydrates.

Archbold & Mukerjee (1942), however, in critical investigations on barley, find that at no time do the roots provide carbohydrate for upward translocation; furthermore, that the amount of soluble carbohydrate in the roots is very small. This situation may be related to the annual and non-persistent habit of barley, since Roberts & Hunt (1936), who continued their cutting experiment on a hay type of *Phleum pratense*, found no evidence of root storage in this plant, any reserve material accumulating above ground in the bulbous base of the shoot.

Detailed biochemical investigations have been made by Sullivan & Sprague (1943), working with *Lolium perenne*. Clonal plants were cut at 1½ in. from ground level, and the stubble and roots analysed for carbohydrates during the 36 days after cutting. It was found that storage material was in the form of the soluble carbohydrates, glucose, sucrose, fructose and fructosans. A steady decline was observed for the first 11 days after cutting, the storage carbohydrates from the roots and stubble being drawn upon for the production of new leaves. After 11 days re-storage of carbohydrate began, and by 28–30 days the concentration of reserves was back to its original level. If plants were kept in complete darkness after cutting depletion of reserves continued until exhaustion and death of the plants occurred. Apparently at least 28–30 days' interval between cuts is required to maintain storage of soluble carbohydrates in the stubble and roots and the maximum exhaustion would occur with an 11-day interval. These results indicate that recovery after cutting is due to a favourable balance between synthesis and storage of carbohydrates in the plant, and their removal by cutting with the subsequent production of new foliage. In the present experiment, where the recovery under fortnightly cuts is significantly less than under monthly cuts for all strains, the fortnightly cut evidently gives too small an interval for re-storage of carbohydrates to their original level. There is no significant difference between recovery after monthly cuts throughout the season and recovery after a flowering date cut followed by monthly cuts. Apparently an interval of 4 weeks gives sufficient time for carbohydrate reserves to be maintained.

The differing productivity of the various strains under cutting treatments may be related to a different partition of carbohydrate between storage in the roots or lowermost nodes and its use in new head and leaf production. In addition, the amount of photosynthetic tissue left after cutting will differ from strain to strain.

In the annual Wimmera and biennial Italian the growth habit is erect. Many of the

nodes, and therefore new tillers, are above the level of cutting. As a result, a 1 in. cut removes most of the photosynthetic tissue and possibly some storage reserves. In Wimmera all tillers rush into head with very little leaf production, and so the amount of photosynthetic tissue is small. It is probable that little, if any, storage in the roots occurs, since Wimmera plants normally die in late summer, even when no cutting is carried out. In Italian, most new tillers head within 20 days, and its abundance of growth is composed mainly of stem shoots, but there is more leaf tissue than in Wimmera and possibly more synthesis and storage of carbohydrates.

With the perennial habit there is rather less head production and more vegetative tillers are formed, this time at ground-level. The habit of growth becomes more prostrate. This means that many of the lower nodes and some photosynthetic tissue will be left below the level of cutting, while later heading may mean less drain on carbohydrate reserves.

C. General conclusions

The different behaviour of the annual and perennial strains can be explained in terms of a balance between, at one extreme, rapid differentiation and elongation of the flowering shoot with inhibition of axillary buds, and, at the other extreme, profuse development of axillary buds as vegetative tillers with comparatively slow differentiation of the inflorescence. This balance acts directly on head production and indirectly, through partition of carbohydrates, on recuperative capacity.

In the annual and biennial, differentiation and elongation of the main shoots are emphasized. The shoot becomes 'ripe to flower' very quickly, as is expressed both by heading in autumn of the seeding year and by continued head production after cutting. This extensive head production may not only lead to withdrawal of food reserves from the roots, but the accompanying decrease of tillering and leaf production means less photosynthetic tissue, hence less storage of reserves. Cutting removes nearly all the leaves and many new tillers, and the meagre reserves in the roots are still further depleted. Complete exhaustion of root reserves may eventually occur.

In the perennials, a longer time is taken for the main shoots to become 'ripe to flower', and the development of axillary buds as vegetative tillers is more pronounced. This results in the absence of heading in autumn of the seeding year, and also in a rapid decline in head production after cutting. Furthermore, the extensive tillering at ground-level means that some leaf tissue remains after cutting and can continue to synthesize carbohydrate. As a result, depletion of the root reserves is far less than in the annual and biennial, and recovery after cutting and persistency are therefore greater.

V. SUMMARY

1. This paper forms part of an investigation on the comparative morphology and physiology of a related group of herbage grasses, the outbreeding species of the genus *Lolium*. It is concerned with the relation between the annual or perennial habit and head production under various intensities of cutting.

2. Six species or strains of *Lolium* were used: *L. rigidum* Gaud. (Wimmera ryegrass); *L. italicum* Braun (Italian ryegrass); and four types of *L. perenne* Linn. (perennial ryegrass), including three bred strains and one commercial type. The four systems of cutting employed were:

(a) Fortnightly cuts beginning 16 April.

(b) Monthly cuts beginning 16 April.

(c) One cut on date of ear emergence, followed by one aftermath flowering date cut and subsequently by monthly cuts.

(d) One cut on the date of flowering, followed by subsequent cuts as in (c) above.

The data collected comprised:

(a) The fresh weight per row of ten plants at each cut.

(b) Leaf-stem percentage in the cut herbage.

(c) The number of heads emerging during each cutting interval.

3. All strains, annual, biennial and perennial, show an initial peak of head production associated with the usual date of ear emergence for the strain.

In the annual Wimmera and biennial Italian, heading continues throughout the summer even under a fortnightly cut. In the bred strains, head production rapidly decreases after the flush associated with ear emergence. The Irish commercial type is intermediate. In all strains a fortnightly cutting severely reduced heading, as compared to the more lenient treatments.

4. The highest total yield in all strains is obtained from the most lenient treatment—date of flowering and subsequent cuts—while yield declines as intensity of cutting increases. For the initial cuts in all treatments, Italian is superior, but as cutting continues, its capacity for recovery declines, and its total yield for the fortnightly cuts is below that of some bred strains. The three bred strains show parallel curves of productivity under all treatments, in spite of their differences in date of emergence. Their recuperative capacity is significantly greater than that of the other three types. In Irish commercial under all treatments, relative productivity decreases after the second cut, and both total yield and recovery are significantly below that of the bred strains. The annual Wimmera gives a low yield in all cases, its herbage being composed mainly of heads. It has a very low recovery after cutting.

5. The normal course of inflorescence development in *Lolium* under field conditions is described, and the effect of cutting on head production is related to the rapidity with which the different strains become 'ripe to flower'. In the field all strains become 'ripe to flower' during winter and begin spikelet differentiation in the spring. Cutting removes all elongating flowering shoots, leaving young axillary tillers. In the annual and biennial these young tillers rapidly become 'ripe to flower' and head before the next cut. In the perennials this condition is attained much more slowly and no further heading may occur in the same season. It is shown that a main tiller can influence the 'ripeness to flower' of its axillary shoots. The effect of head production on tillering in the annual and perennial strains is considered.

6. Seasonal productivity, and in particular recovery after cutting, is discussed in relation to storage and depletion of root reserves. In the present experiment a fortnightly cut gives too small an interval for re-storage of reserves to their original level, but a monthly cut is quite adequate. Recovery after cutting is related to the growth habit and degree of head production of the different strains. In the annual Wimmera and biennial Italian, the habit of growth is erect. Cutting removes most of the leaves and many axillary buds, and the extensive heading is associated with low tillering and leaf production. In the perennial strains, the growth habit is more prostrate and some leaves are left after cutting, together with most of the axillary buds. Heading is less extensive and tillering and leaf production are more pronounced. The effect of heading itself on depletion of root

reserves is not yet clear, but in the perennial strains, head elongation seems to lead to depletion of root reserves.

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THE SPECIFIC CHARACTER OF PLANT COMMUNITIES

I. HERBACEOUS COMMUNITIES

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(With Plates 6 and 7 and one Figure in the Text)

The object of this investigation is to examine the distribution of species in a number of plant communities in order to see if some biometrical standards can be established which may be used to define the specific character of such communities. The analysis has been confined to 'natural' communities of a stable character, where there is no cause to suppose that a major change in the dominant species has occurred for a number of years. In the present paper the method employed in sampling these communities will be described and the results of field surveys will be given, and in a subsequent paper these results will be analysed in order to show that it may be possible to define the specific character of the community by the 'pattern' formed by the species.

Previous work on the quantitative approach to plant ecology has been reviewed by Ashby (1936, 1948), and the status of the plant association and the classification of communities have been discussed by Pavillard (1935). More recently, Fisher, Corbet & Williams (1943) and Williams (1944, 1947) have sought to typify plant and animal populations by the Index of Diversity, a character which was derived from the Logarithmic Series (Fisher *et al.* 1943), and which has also been used by Bond (1947). The basic assumption of the Logarithmic Series is that the species with the least number of individuals are the most numerous. This assumption has been criticized by Preston (1948), who puts forward the alternative hypothesis that the commonest and rarest species are the least frequent and that, in the total population of a community, the distribution of species, with reference to the number of individuals by which they are represented, can be approximated by a normal curve.

The assumptions made by Williams and Preston have led them to far-reaching conclusions, for in both cases their theories were first formulated in connexion with insect and bird populations, and they have subsequently applied them to plant populations using data collected by other workers. It is here assumed, however, that the plant community is limited by a finite area and that the standards adopted in defining the limits of this area are not necessarily applicable to the definition of animal communities. If this assumption is correct then certain fundamental conditions must be observed when sampling plant communities, and these conditions will also have to be observed in any subsequent analysis of the results obtained. A brief review of the standards adopted will show why these precautions are necessary.

THE PLANT COMMUNITY

It is here assumed that in a plant community the dominant species creates, and is associated with, conditions which more or less determine the extent of the area and the kind and relative abundance of the remaining species in the community. That is to say, given

uniform climatic, topographic and edaphic conditions, it is considered that the dominant species is the most important factor in determining the character of the community. The recognition of the dominant is, however, largely subjective for it cannot be said that the largest species in the community is the dominant; this is particularly evident in a herbaceous community such as a chalk-grassland; nor can it be said that the most frequent species is the dominant, for where there is a great difference in the life form of the species, as in a woodland community, this would again be untrue; and it very rarely happens that the largest species is also numerically the commonest. It is probably true, however, that the total area covered by the individuals of the dominant, either by virtue of crown size or basal area, is greater than that covered by the individuals of any other species. However, the percentage area covered is very difficult to estimate and there is no general agreement about the method to be employed, so for the purpose of the present discussion it may be considered that the selection of the dominant has been entirely subjective.

It is assumed, therefore, that only the area over which the species is actually influential as a dominant can be considered to fall within the boundaries of the community. If this be true then at any period of observation the community must be represented by a finite area and a finite number of species.

In actual practice, in order to check the limits of the community, an inspection was carried out by automatically making a rough estimate of the amount of cover or number of individuals of the dominant species in representative samples. In this way the boundaries of the community were marked out, and subsequent sampling was confined strictly to this area.

SAMPLING

In order to estimate the specific character of the community it is necessary to know the increase in the average number of species per unit area with progressive increase of the unit area considered. For this purpose samples of different sizes were taken and only the presence of the species within the sample area was noted, as it was the species and not the individual which was to be treated as the statistical unit.

Various shapes and sizes of sample area have been employed as, for example, the infinitesimally small area or point advocated by Levy & Madden (1933), the circle of 0.01 sq.m. used by Raunkiaer (1934), the belt or strip favoured by Clapham (1932) and Pidgeon & Ashby (1940), and the square quadrat used by the majority of workers. For the present investigation the square quadrat was used as the size of the sample could easily be increased without altering the proportion of the sides.

In all cases twenty samples of each quadrat size were taken; this was considered a sufficient number as the average number of species per unit area rapidly becomes constant (Raunkiaer, 1934). It is worth while noting that it is essential to keep the number of samples constant if results from quadrats of different sizes are to be compared.

The multiple quadrat

In order to carry out the sampling quickly and accurately it was necessary to have some sort of light portable frame which, when unfolded, would open out a network of different-sized squares.

The quadrat took the form of a metal framework, of channel section, across which were

stretched fine strings forming squares of any desired size. To facilitate transport the framework was designed to fold by arranging hinges at the corners in a very special way.

In Fig. 1a, *AB*, *BC*, *CD*, *DA* are the sides of the square framework. At the corners *D* and *B* are hinges which have their axes in the plane of the figure. At *A* and *C* are hinges with their axes perpendicular to the plane of the figure.

Thus, when the framework is folded on the axis *DB* so that the corners *A* and *C* coincide (Fig. 1b), the axes of the hinges *A* and *C* are in line and permit the corners *B* and *D* to turn into coincidence, or nearly so (Fig. 1c).

The flexible strings are relieved of tension immediately folding begins, and look after themselves. When unfolding the instrument they are pulled straight and tight, the framework being stiff enough for this purpose, thus giving a perfectly constant mesh under all field conditions, in other words, a reliable standard portable multiple quadrat.

It is necessary to add that the lugs at *e* and *f* perform the following essential functions: they carry two holes 1 and 2, forming a wide and stable base whereby the quadrat can be

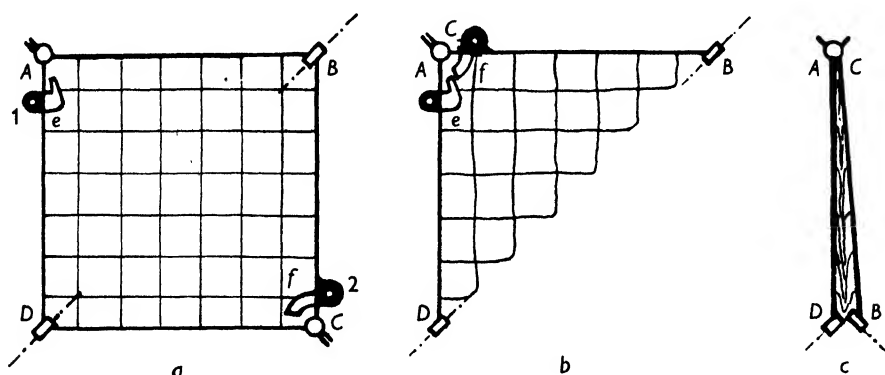


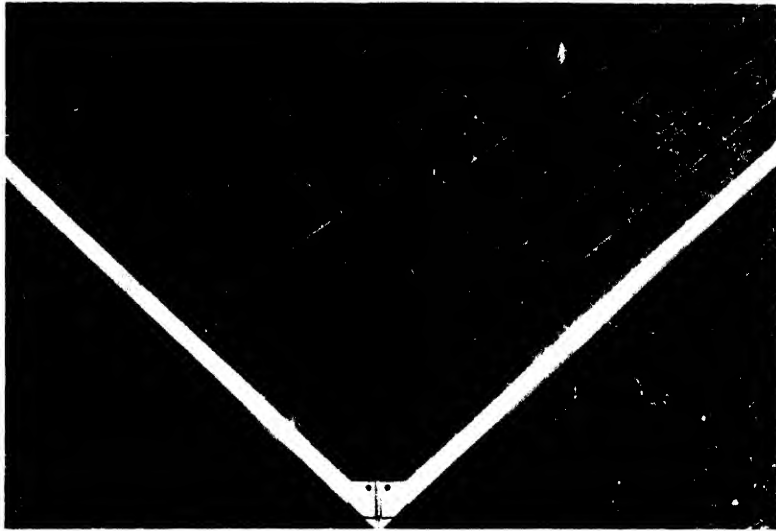
Fig. 1. The folding mechanism of the framework of the multiple quadrat. *a*, Quadrat open, all strings taut. *e* and *f*, lugs of safety gate. 1 and 2, holes for securing quadrat to ground. *b*, end of first movement, tension in strings relaxed. *c*, end of second movement, strings fold automatically in space *AD-BC*.

fixed during any set of observations. They are also shaped and positioned so as to form a gate which will prevent the quadrat from being opened until the hinges at *B* and *D* are in alinement. When folded to the position shown in Fig. 1b, lug *f* is in a plane just below the level of lug *e* and passes underneath *e* during the transition from the position shown in Fig. 1b to that shown in Fig. 1c. The lugs are not drawn to scale and for clarity are omitted from Fig. 1c.

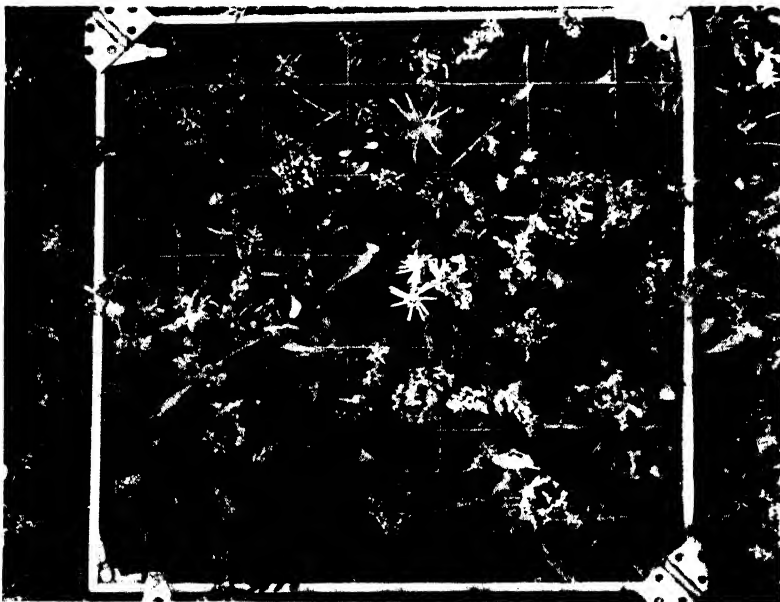
Without the safety gate the instrument is liable to be severely strained should the second movement of opening out the frame be commenced a little too soon.

The multiple quadrat used in this investigation provided squares of 25, 625, 2500 sq.cm. and 1 sq.m. A smaller square of 1 sq.cm. was later added and, when the type of community permitted, larger squares of 4, 16 and 64 sq.m. were marked out with tapes.

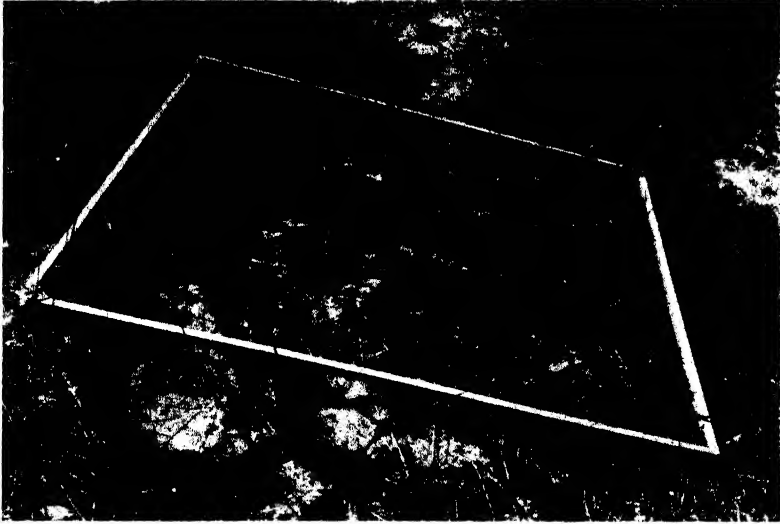
Samples were taken at random within the community by throwing a skewer so as to get the position of the smallest square in one corner of the multiple quadrat, and as each succeeding size of square enclosed the previous one it was only necessary to list the new species which occurred in each additional area. This method is accurate and fairly rapid as large quadrats are split up into a number of sections which can be examined methodically.



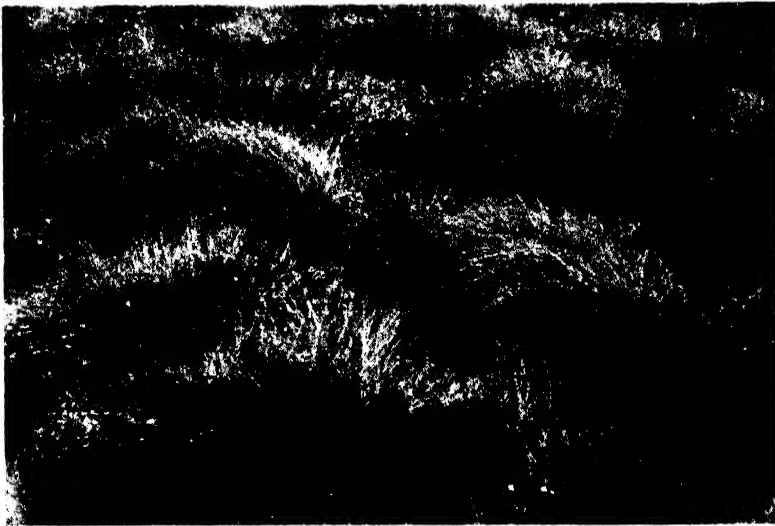
Phot. 1. *Salicornia* marsh, Blakeney Point, Norfolk, June 1948. *Salicornia stricta* and *Pelvetia canaliculata* (dark patches) form a dense mat which covers the ground almost completely. Small squares of quadrat equal to 25 sq.cm.



Phot. 2. *Limonium*, marsh Blakeney Point, Norfolk, June 1948. *Limonium vulgare* and *Aster tripolium* in flower. The matted appearance is due to the fine leaves of *Plantago maritima*, *Armeria maritima*, *Triglochin maritimum* and *Puccinellia maritima*. Small squares of quadrat equal to 20 sq.cm.



Phot. 3. *Psamma* dune, Blakeney Point, Norfolk, June 1948. Patches of *Hypnum cupressiforme* var. *tectorum*, *Ceratodon purpureum* and *Tortula ruraliformis* between small tussocks of *Ammophila arenaria*. Folding frame for quadrats up to 1 sq.m.



Phot. 4. *Eriophorum* bog, Ringinglow, Sheffield, August 1948. The photograph shows the large tussocks of *Eriophorum vaginatum* and the inflorescences of *Deschampsia flexuosa*. The channels between the tussocks are hidden by the *Eriophorum* leaves.

It will be seen that the samples are not entirely independent of each other, but on several occasions when communities were sampled by taking quadrat sizes independently, it was found that the general form of the species-area curve was in no way different from the curves obtained when the multiple quadrat method was used.

THE COMMUNITIES SAMPLED

The communities sampled are listed in Table 1. They are forms of well-known natural communities of a more or less stable character and represent a wide range of edaphic conditions varying from dune and salt-marsh to chalk and mountain grassland. They were chosen for their uniformity of life form, being composed predominantly of herbaceous angiosperm types. This choice reduced the problem of sampling to its simplest form since the difficulties caused by widely differing life forms did not have to be considered.

The degree of cover in these communities varied from less than one-sixth in the *Honkenya* community to more or less complete cover in the chalk grasslands and mountain grassland. Tussock forms were represented in the Psamma dune by *Ammophila arenaria*, in the cotton-grass bog by *Eriophorum vaginatum* and in the mountain grassland by *Nardus stricta*. Mosses, liverworts and lichens, when present, were also included in the frequency counts. Photographs of some of the communities are given in Pls. 6 and 7, photos. 1-4, and the statistics for the number of individuals per unit area for the *Salicornia* marsh, *Limonium* marsh, *Glaux* low, *Carex* dune and *Festuca* chalk grassland have been dealt with in previous publications (Archibald, 1948, 1949).

Table 1. *Communities sampled*

Community	Locality	Date of sampling	Approximate area of community (acres)
<i>Salicornia</i> marsh	Blakeney Point, Norfolk	June-July 1948	1.0
<i>Limonium</i> marsh	Blakeney Point, Norfolk	June-July 1948	2.0
<i>Honkenya</i> shingle	Blakeney Point, Norfolk	June-July 1948	0.25
<i>Carex</i> dune	Blakeney Point, Norfolk	June-July 1948	0.25
<i>Glaux</i> low	Blakeney Point, Norfolk	June-July 1948	0.25
Psamma dune	Blakeney Point, Norfolk	June-July 1948	2.0
<i>Eriophorum</i> bog	Ringinglow Bog, Sheffield	August 1948	2.0
<i>Nardus</i> grassland	Wrynose Pass, Westmorland	August 1948	2.0
<i>Festuca</i> chalk grassland	Bledlow, Oxford	June 1948	0.25
(<i>Helianthemum</i> - <i>Thymus</i>)			
<i>Festuca</i> chalk grassland	Pitstone, Buckingham	August 1948	2.0
(<i>Linum</i> - <i>Briza</i> - <i>Koeleria</i>)			

RESULTS OF FIELD SURVEYS

A list of the species in each community, together with the observed frequency of occurrence of each species in samples of different sizes, is given in Tables 2-11. The total number of species for each community includes all the species sampled, with the addition of any rare species which occurred within the limits of the community but which were not encountered in the random selection of sample areas.

In communities where the average number of species per unit area was large it was not possible to examine very large quadrats, but the figures given in the tables show that in all cases the largest area sampled includes an average of half, or very nearly half, the total number of species in the community.

There is a noticeable difference between the communities with regard to the total number of species by which each is represented. The smallest numbers occur in the maritime communities which are inundated by salt water, for there are only twelve species in the *Salicornia* marsh, which is covered by all but the lowest tides, and fifteen in the *Limonium* marsh, which is inundated only by the highest tides. The largest number of species was found in the *Festuca* chalk grasslands, there being fifty-one in the Bledlow community, where *Helianthemum nummularium* and *Thymus serpyllum* were very conspicuous, and sixty-seven in the Pitstone community, where *Linum catharticum*, *Briza media* and *Koeleria gracilis* were of most frequent occurrence next to *Festuca*.

Before concluding the present section it is worth while noting that this method of sampling gives some useful information about the commonness and rarity of occurrence of the species in each community.

Table 2. *Salicornia* marsh

NOTE. Plant names are according to the *Check-list of British Vascular Plants* (Clapham, 1946).

Species	Frequency for twenty samples							
	Sq.cm.				Sq.m.			
	1	25	625	2500	1	4	16	64
1. <i>Aster tripolium</i>	1	1	7	14	20	20	20	20
2. <i>Limonium vulgare</i>	—	—	1	2	3	4	12	19
3. <i>Obione portulacoides</i>	—	—	—	—	—	1	6	9
4. <i>Salicornia stricta</i>	19	20	20	20	20	20	20	20
5. <i>Spergularia marginata</i>	—	—	—	—	1	1	7	12
6. <i>Salicornia</i> sp.	—	—	—	—	—	1	3	5
7. <i>Plantago maritima</i>	—	—	—	—	—	1	1	1
8. <i>Suaeda maritima</i>	1	2	5	8	16	19	20	20
9. <i>Puccinellia maritima</i>	—	—	—	—	—	—	3	8
10. <i>Triglochin maritimum</i>	—	—	—	—	—	1	4	8
11. <i>Bostrychia scorpioides</i>	6	8	14	17	18	20	20	20
12. <i>Pelvetia canaliculata</i>	16	20	20	20	20	20	20	20
Total frequency	43	51	67	81	98	108	136	162
Average per quadrat	2.15	2.55	3.35	4.05	4.85	5.4	6.8	8.1

Table 3. *Limonium* marsh

Species	Frequency for twenty samples							
	Sq.cm.				Sq.m.			
	1	25	625	2500	1	4	16	64
1. <i>Armeria maritima</i>	3	10	19	20	20	20	20	20
2. <i>Artemisia maritima</i>	—	—	—	—	2	—	2	4
3. <i>Aster tripolium</i>	1	6	15	17	18	20	20	20
4. <i>Cochlearia officinalis</i>	1	4	12	17	19	20	20	20
5. <i>Glaux maritima</i>	—	—	—	1	1	—	—	—
6. <i>Limonium vulgare</i>	10	19	20	20	20	20	20	20
7. <i>Obione portulacoides</i>	—	1	7	15	19	20	20	20
8. <i>Plantago maritima</i>	9	13	19	19	19	20	20	20
9. <i>Salicornia stricta</i>	5	16	19	19	20	20	20	20
10. <i>Suaeda maritima</i>	2	14	19	20	20	20	20	20
11. <i>Spergularia marginata</i>	—	4	8	13	15	20	20	20
12. <i>Festuca rubra</i>	—	4	7	11	13	15	18	19
13. <i>Lepturus</i> sp.	—	1	1	2	2	2	4	5
14. <i>Puccinellia maritima</i>	1	7	15	17	17	20	20	20
15. <i>Triglochin maritimum</i>	2	14	20	20	20	20	20	20
Total frequency	34	113	181	211	225	237	244	248
Average per quadrat	1.7	5.65	9.05	10.55	11.25	11.85	12.2	12.4

Table 4. *Honkenya shingle*

Species	Frequency for twenty samples							
	Sq.cm.				Sq.m.			
	1	25	625	2500	1	4	16	64
1. <i>Anagallis arvensis</i>	—	—	—	—	4	5	5	7
2. <i>Arenaria</i> sp.	—	—	—	—	—	1	4	6
3. <i>Armeria maritima</i>	—	—	—	1	4	4	13	19
4. <i>Atriplex</i> sp.	—	—	4	12	16	20	20	20
5. <i>Cerastium semidecandrum</i>	—	—	—	—	—	1	3	4
6. <i>Honkenya peploides</i>	6	16	20	20	20	20	20	20
7. <i>Limonium binervosum</i>	—	—	—	—	—	4	9	15
8. <i>Plantago coronopus</i>	—	—	—	—	—	1	1	1
9. <i>Salsola kali</i>	—	—	—	—	—	—	—	1
10. <i>Sedum acre</i>	—	—	—	—	—	2	3	3
11. <i>Senecio jacobaea</i>	—	—	—	—	—	—	1	2
12. <i>Silene maritima</i>	—	1	2	3	7	10	19	20
13. <i>Suaeda fruticosa</i>	—	—	—	1	4	—	1	2
14. <i>Suaeda maritima</i>	—	—	—	1	1	1	2	4
15. <i>Aira praecox</i>	—	—	—	—	—	—	—	1
16. <i>Agropyron junceum</i>	—	—	—	2	2	10	17	20
17. <i>Festuca rubra</i>	—	—	—	—	—	2	2	2
18. <i>Phleum arenarium</i>	—	—	—	2	2	2	4	5
19. <i>Poa</i> sp.	—	—	—	—	—	1	1	1
20. <i>Desmazeria loliacea</i>	—	—	—	—	—	—	1	2
21. <i>Ceratodon purpureum</i>	—	—	—	—	—	—	1	2
Additional species								
22. <i>Poa</i> sp.	—	—	—	—	—	—	—	—
Total frequency	6	17	26	42	56	83	126	157
Average per quadrat	0.3	0.85	1.3	2.1	2.8	4.15	6.3	7.85

Table 5. *Carex dune*

Species	Frequency for twenty samples			
	Sq.cm.			Sq.m.
	25	625	2500	1
1. <i>Erodium cicutarium</i>	—	—	1	4
2. <i>Carex arenaria</i>	16	20	20	20
3. <i>Festuca rubra</i>	2	6	11	13
4. <i>Phleum arenarium</i>	—	—	—	3
5. <i>Brachythecium albicans</i>	1	2	2	2
6. <i>Dicranum scoparium</i> v. <i>orthophyllum</i>	6	7	10	12
7. <i>Hypnum cupressiforme</i>	12	19	19	19
8. <i>Ceratodon purpureum</i>	—	—	1	1
9. <i>Cephaloziella starkii</i>	—	3	3	3
10. <i>Cladonia furcata</i>	13	19	20	20
11. <i>Cladonia foliacea</i>	15	20	20	20
12. <i>Cladonia pyxidata</i>	3	6	8	11
13. <i>Cladonia</i> sp.	2	6	9	14
14. <i>Cladonia</i> sp.	12	20	20	20
15. <i>Cladonia</i> sp.	2	7	9	12
16. <i>Cladonia</i> sp.	—	—	2	5
17. <i>Cladonia</i> sp.	—	1	2	4
18. <i>Parmelia physodes</i>	—	—	2	5
Additional species				
19. <i>Aira praecox</i>	—	—	—	—
20. <i>Erophila verna</i>	—	—	—	—
21. <i>Myosotis collina</i>	—	—	—	—
22. <i>Peltigera</i> sp.	—	—	—	—
Total frequency	84	136	159	188
Average per quadrat	4.2	6.8	7.95	9.4

Table 6. *Glaux low*

Species	Frequency for twenty samples							
	Sq.cm.				Sq.m.			
	1	25	625	2500	1	4	16	64
1. <i>Anagallis arvensis</i>	—	—	—	—	—	—	1	11
2. <i>Atriplex</i> sp.	—	—	—	—	1	1	2	2
3. <i>Cirsium vulgare</i>	—	—	—	—	—	2	7	9
4. <i>Cerastium semidecandrum</i>	—	—	—	—	—	—	2	5
5. <i>Epilobium</i> sp.	—	—	—	1	3	3	3	3
6. <i>Glaux maritima</i>	14	19	20	20	20	20	20	20
7. <i>Hydrocotyle vulgare</i>	—	—	—	—	—	—	1	1
8. <i>Limonium binervosum</i>	—	—	—	—	2	2	4	4
9. <i>Myosotis collina</i>	—	—	—	—	—	—	—	1
10. <i>Plantago coronopus</i>	3	15	19	20	20	20	20	20
11. <i>Sagina</i> sp.	4	16	20	20	20	20	20	20
12. <i>Sedum acre</i>	—	—	1	7	9	4	8	10
13. <i>Senecio jacobaea</i>	—	3	12	17	19	20	20	20
14. <i>Sonchus</i> sp.	—	—	—	—	—	3	8	13
15. <i>Agropyron junceum</i>	—	—	—	—	—	1	6	11
16. <i>Agrostis</i> sp.	—	—	—	1	2	3	9	19
17. <i>Aira praecox</i>	—	1	2	2	2	1	3	8
18. <i>Ammophila arenaria</i>	—	—	—	—	—	—	—	5
19. <i>Carex</i> sp.	—	—	—	1	3	—	3	9
20. <i>Cynosurus cristatus</i>	—	—	—	—	—	2	5	14
21. <i>Festuca rubra</i>	—	—	1	1	1	3	11	16
22. <i>Juncus bufonis</i>	1	5	14	18	19	20	20	20
23. <i>Juncus gerardii</i>	—	—	—	—	2	12	15	16
24. <i>Holcus</i> sp.	—	—	—	—	—	—	—	2
25. <i>Koeleria</i> sp.	—	—	—	—	—	1	1	1
26. <i>Orchid</i>	—	—	—	—	—	—	1	1
27. <i>Phleum arenarium</i>	—	—	6	8	10	8	10	18
28. <i>Poa annua</i>	1	4	12	14	16	19	20	20
29. <i>Poa</i> sp.	—	—	—	—	—	—	—	1
30. <i>Puccinellia maritima</i>	—	—	1	1	3	7	10	12
31. <i>Desmazeria loliacea</i>	—	—	4	4	6	13	14	18
32. <i>Triglochin maritimum</i>	—	—	—	—	—	6	7	12
33. <i>Aneura pinguis</i>	1	4	9	11	13	17	18	19
34. <i>Brachythecium albicans</i>	—	2	7	8	12	6	10	17
35. <i>Bryum</i> sp.	8	16	20	20	20	20	20	20
36. <i>Ceratodon purpureum</i>	1	5	8	11	14	16	17	18
Total frequency	33	90	156	185	217	250	316	416
Average per quadrat	1.65	4.5	7.8	9.25	10.85	12.5	15.8	20.8

Table 7. *Psamma dune*

Species	Frequency for twenty samples							
	Sq.cm.				Sq.m.			
	1	25	625	2500	1	4	16	64
1. <i>Cirsium vulgare</i>	—	—	—	—	—	1	3	4
2. <i>Cerastium semidecandrum</i>	—	1	9	14	17	18	19	20
3. <i>Cerastium tetrandrum</i>	—	2	5	6	10	10	13	17
4. <i>Cynoglossum officinale</i>	—	—	—	—	—	1	2	2
5. <i>Erodium cicutarium</i>	—	—	—	—	—	4	11	14
6. <i>Erophila verna</i>	—	1	3	10	14	8	12	17
7. <i>Geranium molle</i>	—	—	—	—	—	—	1	1
8. <i>Hypochaeris radicata</i>	—	—	—	—	—	—	—	2
9. <i>Myosotis collina</i>	—	1	6	13	17	16	19	20
10. <i>Rumex acetosella</i>	—	—	—	—	—	—	1	1
11. <i>Sagina</i> sp.	—	—	—	—	—	1	1	2
12. <i>Salsola kali</i>	—	—	—	—	—	—	—	1
13. <i>Sedum acre</i>	—	—	—	—	—	10	12	15
14. <i>Senecio jacobaea</i>	—	—	8	15	19	20	20	20
15. <i>Silene maritima</i>	—	—	—	—	—	1	2	3
16. <i>Stellaria apetala</i>	—	2	3	5	10	17	20	20
17. <i>Aira praecox</i>	—	—	4	4	4	6	10	15
18. <i>Agropyron junceum</i>	—	—	—	—	1	3	3	6
19. <i>Ammophila arenaria</i>	4	12	20	20	20	20	20	20
20. <i>Festuca rubra</i>	1	7	20	20	20	20	20	20
21. <i>Holcus</i> sp.	—	—	—	—	—	—	—	1
22. <i>Phleum arenarium</i>	—	—	—	2	6	6	9	13
23. <i>Poa</i> sp.	—	—	—	—	—	—	2	4
24. <i>Polypodium vulgare</i>	—	—	—	—	—	—	—	1
25. <i>Brachythecium albicans</i>	9	12	16	18	18	20	20	20
26. <i>Bryum</i> sp.	—	2	5	6	9	—	—	—
27. <i>Ceratodon purpureum</i>	4	7	11	15	18	19	19	19
28. <i>Dicranum scoparium</i> v. <i>orthophyllum</i>	—	1	1	2	2	4	6	8
29. <i>Hypnum cupressiforme</i> v. <i>tectorum</i>	1	3	5	7	10	9	12	16
30. <i>Tortula ruraliformis</i>	2	2	7	10	14	18	20	20
31. Unidentified moss	—	—	—	—	—	—	1	2
32. <i>Cephaloziella starkii</i>	—	1	1	1	1	—	—	—
33. <i>Cladonia furcata</i>	1	2	10	14	16	16	17	19
34. <i>Cladonia pyxidata</i>	1	6	11	13	15	9	15	15
35. <i>Cladonia</i> sp.	—	—	1	4	4	6	15	18
36. <i>Cladonia</i> sp.	—	—	—	—	—	1	1	1
37. <i>Parmelia physodes</i>	—	—	1	2	3	3	10	15
38. <i>Peltigera</i> sp.	—	1	8	13	14	11	15	17
39. <i>Parmelia</i> sp.	—	—	—	—	1	4	5	13
40. <i>Compositae</i>	—	—	—	—	—	4	5	5
Total frequency	24	63	155	214	264	286	362	441
Average per quadrat	1.2	3.15	7.75	10.7	13.2	14.3	18.1	22.05

Table 8. *Eriophorum bog*

Species	Frequency for twenty samples							
	Sq.cm.				Sq.m.			
	1	25	625	2500	1	4	16	64
1. <i>Calluna vulgaris</i>	—	1	1	3	4	9	15	20
2. <i>Empetrum nigrum</i>	—	—	2	2	2	3	3	13
3. <i>Erica tetralix</i>	—	—	—	—	—	—	—	4
4. <i>Oxycoccus quadripetalus</i>	—	—	3	3	4	4	7	13
5. <i>Deschampsia flexuosa</i>	6	8	20	20	20	20	20	20
6. <i>Eriophorum angustifolium</i>	—	—	1	3	4	7	8	10
7. <i>Eriophorum vaginatum</i>	9	15	20	20	20	20	20	20
8. <i>Dryopteris</i> sp.	—	—	—	—	—	—	—	1
9. <i>Campylopus atrovirens</i>	—	—	—	1	1	2	5	6
10. <i>Dicranella heteromella</i>	—	—	2	4	8	16	17	18
11. <i>Plagiothecium elegans</i>	—	—	—	—	—	—	—	4
12. <i>Polytrichum gracile</i>	—	—	—	—	—	—	—	3
13. <i>Sphagnum recurvum</i>	—	—	—	—	—	—	1	2
14. <i>Sphagnum rubellum</i>	—	—	—	—	—	—	—	1
15. <i>Webera nutans</i>	—	2	7	16	20	20	20	20
16. <i>Calypogeia trichomanes</i>	1	2	9	14	17	20	20	20
17. <i>Cephalozia bicuspidata</i>	1	2	5	7	15	19	20	20
18. <i>Lepidozia reptans</i>	—	—	—	—	—	1	1	1
19. <i>Gymnocolea inflata</i>	—	—	—	—	—	—	1	4
20. <i>Cladonia</i> sp.	—	2	2	5	5	10	12	14
21. <i>Cladonia</i> sp.	—	—	—	—	—	—	—	2
Additional species								
22. <i>Vaccinium myrtillus</i>	—	—	—	—	—	—	—	—
Total frequency	17	32	72	98	120	151	170	216
Average per quadrat	0.85	1.6	3.6	4.9	6.0	7.55	8.5	10.8

Table 9. *Nardus grassland*

Species	Frequency for twenty samples				Sq.m. 1
	Sq.cm.				
	1	25	625	2500	
1. <i>Calluna vulgaris</i>	—	—	—	—	1
2. <i>Empetrum nigrum</i>	—	—	—	1	1
3. <i>Galium saxatile</i>	2	7	19	20	20
4. <i>Potentilla erecta</i>	—	1	10	14	18
5. <i>Vaccinium myrtillus</i>	—	2	8	12	15
6. <i>Agrostis</i> sp.	7	13	19	20	20
7. <i>Agrostis</i> sp.	—	—	—	1	1
8. <i>Anthoxanthum odoratum</i>	—	1	6	6	8
9. <i>Carex panicea</i>	—	—	2	3	7
10. <i>Carex</i> sp.	—	1	4	12	14
11. <i>Deschampsia flexuosa</i>	4	8	11	11	14
12. <i>Festuca ovina</i>	9	14	20	20	20
13. <i>Juncus squarrosus</i>	—	—	3	5	10
14. <i>Luzula campestris</i>	—	—	—	5	10
15. <i>Nardus stricta</i>	8	15	20	20	20
16. <i>Narthecium ossifragum</i>	—	1	2	4	6
17. <i>Scirpus cespitosus</i>	—	1	2	2	4
18. <i>Sieglingia decumbens</i>	1	1	6	7	11
19. <i>Lycopodium selago</i>	—	—	1	1	1
20. <i>Dicranum scoparium</i>	—	1	5	7	10
21. <i>Hylocomium squarrosum</i>	1	3	9	9	14
22. <i>Hylocomium triquetrum</i>	1	1	9	10	13
23. <i>Hypnum cupressiforme</i>	7	10	13	15	18
24. <i>Hypnum schreberi</i>	4	9	16	19	20
25. <i>Hypnum splendens</i>	—	1	6	9	16
26. <i>Plagiothecium undulatum</i>	—	1	1	4	6
27. <i>Polytrichum commune</i>	3	5	12	15	18
28. <i>Polytrichum strictum</i>	—	—	—	2	6
29. <i>Rhacomitrium</i> sp.	—	—	—	—	1
30. <i>Thuidium tamariscinum</i>	—	—	1	1	3
31. <i>Sphagnum</i> sp.	—	—	1	1	1
32. <i>Sphagnum papillosum</i>	—	—	—	1	1
33. <i>Calypogeia trichomanes</i>	1	3	4	6	9
34. <i>Diplophyllum albicans</i>	—	—	1	3	7
35. <i>Lophocolea bidentata</i>	2	4	10	12	16
36. <i>Lophozia floerkii</i>	1	4	8	13	19
37. <i>Ptilidium ciliare</i>	—	3	3	3	8
38. <i>Cladonia pyxidata</i>	—	—	—	1	2
Total frequency	51	110	232	295	389
Average per quadrat	2.55	5.5	11.6	14.7	19.45

Table 10. *Festuca chalk grassland (Bledlow)*

Species	Frequency of twenty samples			Sq.m. 1
	Sq.cm.			
	25	625	2500	
1. <i>Achillea millefolium</i>	2	7	8	9
2. <i>Campanula rotundifolia</i>	4	11	12	15
3. <i>Carlina vulgaris</i>	1	1	2	3
4. <i>Cirsium acaulos</i>	1	5	11	14
5. <i>Daucus carota</i>	—	3	7	11
6. <i>Galium verum</i>	4	6	11	11
7. <i>Galium aparine</i>	—	—	—	1
8. <i>Gentiana amarella</i>	1	1	1	1
9. <i>Helianthemum nummularium</i>	19	20	20	20
10. <i>Hieracium pilosella</i>	5	6	7	9
11. <i>Hippocrepis comosa</i>	1	—	1	1
12. <i>Leontodon hispidus</i>	5	17	20	20
13. <i>Linum catharticum</i>	6	14	17	19
14. <i>Lotus corniculatus</i>	10	15	16	20
15. <i>Medicago lupulina</i>	2	4	6	8
16. <i>Plantago lanceolata</i>	—	3	10	16
17. <i>Polygala calcarea</i>	—	1	2	4
18. <i>Poterium sanguisorba</i>	—	—	—	4
19. <i>Primula vera</i>	—	1	1	1
20. <i>Prunella vulgaris</i>	1	2	2	3
21. <i>Ranunculus bulbosus</i>	—	2	2	10
22. <i>Rumex</i> sp.	—	—	—	1
23. <i>Scabiosa columbaria</i>	—	2	7	11
24. <i>Senecio jacobaea</i>	1	5	9	15
25. <i>Sonchus oleraceus</i>	—	1	1	1
26. <i>Compositae</i>	—	—	1	1
27. <i>Thymus serpyllum</i>	16	20	20	20
28. <i>Veronica</i> sp.	—	—	1	2
29. <i>Agrostis</i> sp.	—	1	3	5
30. <i>Anthoxanthum odoratum</i>	—	1	1	2
31. <i>Briza media</i>	13	16	19	19
32. <i>Carex caryophylla</i>	1	4	8	10
33. <i>Carex flacca</i>	12	20	20	20
34. <i>Cynosurus cristatus</i>	—	2	4	4
35. <i>Festuca ovina</i>	20	20	20	20
36. <i>Helictotrichon pratense</i>	4	14	15	19
37. <i>Helictotrichon pubescens</i>	2	10	13	13
38. <i>Holcus</i> sp.	—	1	1	1
39. <i>Koeleria gracilis</i>	11	19	20	20
40. <i>Luzula campestris</i>	1	4	5	5
41. <i>Brachythecium purum</i>	3	10	13	16
42. <i>Bryum capillare</i>	—	1	2	4
43. <i>Camptothecium lutescens</i>	—	4	5	8
44. <i>Dicranum scoparium</i>	1	2	4	5
45. <i>Encalypta streptocarpa</i>	—	—	1	1
46. <i>Fissidens</i> sp.	—	1	6	7
47. <i>Mnium</i> sp.	—	1	3	3
48. <i>Hylocomium laurum</i>	15	18	19	19
49. <i>Hypnum cuspidatum</i>	5	11	16	17
50. <i>Hypnum cupressiforme</i>	—	—	1	2
Additional species				
51. Unidentified umbelliferae	—	—	—	—
Total frequency	166	307	393	471
Average per quadrat	8.3	15.35	19.6	23.55

Table 11. *Festuca chalk grassland (Pitstone)*

Species	Frequency for twenty samples				Sq.m.
	Sq.cm.				
	1	25	625	2500	
1. <i>Achillea millefolium</i>	—	—	2	3	3
2. <i>Anthyllis vulneraria</i>	—	—	1	1	3
3. <i>Asperula cynanchica</i>	3	11	16	18	20
4. <i>Bellis perennis</i>	—	2	4	5	8
5. <i>Campanula rotundifolia</i>	1	8	16	20	20
6. <i>Campanula glomerata</i>	—	—	3	6	6
7. <i>Carlina vulgaris</i>	—	1	2	6	12
8. <i>Centaurea nigra</i>	—	—	3	11	16
9. <i>Centaurea scabiosa</i>	—	—	1	1	1
10. <i>Chrysanthemum leucanthemum</i>	—	3	6	10	14
11. <i>Cirsium acaulos</i>	—	5	15	20	20
12. <i>Crataegus oxycanthoides</i> (seedling)	—	—	—	2	3
13. <i>Daucus carota</i>	—	2	5	5	12
14. <i>Euphrasia officinalis</i> agg.	—	—	7	10	13
15. <i>Galium verum</i>	—	1	8	9	16
16. <i>Gentiana amarella</i> agg.	—	2	10	16	16
17. <i>Gymnadenia conopsea</i>	—	—	1	8	13
18. <i>Hieracium pilosella</i>	—	7	15	20	20
19. <i>Hippocrepis comosa</i>	1	4	8	9	10
20. <i>Leontodon hispidus</i>	1	3	17	19	20
21. <i>Linum catharticum</i>	—	10	20	20	20
22. <i>Lotus corniculatus</i>	2	13	19	19	20
23. <i>Medicago lupulina</i>	—	—	—	—	2
24. <i>Ononis spinosa</i>	—	1	8	10	14
25. <i>Pimpinella saxifraga</i>	—	5	15	15	19
26. <i>Plantago media</i>	—	—	11	18	20
27. <i>Plantago lanceolata</i>	—	5	18	19	20
28. <i>Polygala calcarea</i>	—	—	1	2	2
29. <i>Poterium sanguisorba</i>	—	—	1	1	3
30. <i>Primula veris</i>	—	—	1	1	1
31. <i>Prunella vulgaris</i>	—	3	8	14	19
32. <i>Ranunculus bulbosus</i>	—	1	15	19	20
33. <i>Scabiosa columbaria</i>	—	4	15	19	19
34. <i>Senecio jacobaea</i>	—	—	—	1	1
35. <i>Thymus serpyllum</i>	3	10	19	20	20
36. <i>Trifolium pratense</i>	—	—	3	7	17
37. <i>Trifolium repens</i>	—	1	4	6	9
38. <i>Briza media</i>	3	12	20	20	20
39. <i>Bromus erectus</i>	—	7	18	19	19
40. <i>Carex caryophylla</i>	—	2	9	13	18
41. <i>Carex flacca</i>	3	12	19	20	20
42. <i>Festuca ovina</i>	9	20	20	20	20
43. <i>Helictotrichon pratense</i>	3	11	19	20	20
44. <i>Helictotrichon pubescens</i>	1	3	5	9	10
45. <i>Koeleria gracilis</i>	6	16	20	20	20
46. <i>Phleum nodosum</i>	—	—	—	—	1
47. <i>Trisetum flavescens</i>	—	—	2	2	2
48. <i>Brachythecium purum</i>	—	3	9	12	18
49. <i>Bryum</i> sp.	—	—	1	1	1
50. <i>Camptothecium lutescens</i>	—	—	1	3	4
51. <i>Fissidens adiantoides</i>	7	13	18	20	20
52. <i>Hypnum chrysophyllum</i>	5	6	10	10	14
53. <i>Hypnum cuspidatum</i>	—	—	4	7	8
54. <i>Hypnum molluscum</i>	—	—	2	7	9
55. <i>Phascum curvicolle</i>	—	—	1	1	2
56. <i>Weisia sterilis</i> ?	—	—	2	4	5
Additional species					
57. <i>Rosa</i> sp.	—	—	—	—	—
58. <i>Arenaria</i> sp.	—	—	—	—	—
59. Compositae	—	—	—	—	—
60. <i>Festuca rubra</i>	—	—	—	—	—
61. <i>Barbula unguiculata</i> ?	—	—	—	—	—
62. Unidentified moss 1	—	—	—	—	—
63. Unidentified moss 2	—	—	—	—	—
64. <i>Cladonia pyxidata</i> ?	—	—	—	—	—
65. <i>Cladonia</i> sp.	—	—	—	—	—
66. <i>Parmelia</i> sp.	—	—	—	—	—
67. Unidentified lichen	—	—	—	—	—
Total frequency	48	209	476	599	700
Average per quadrat	2.4	10.45	23.8	29.95	35.0

Commonness and rarity of species

It is assumed here that a species can be termed constant when it occurs in 95% or more of the samples taken at random within the community. The species with the greatest number of individuals will be the first to become constant and therefore commonness can be defined by the smallest area on which a species becomes constant. For example, in the *Salicornia* marsh (Table 2), *S. stricta* is the commonest species as it is the first species to become constant on samples of 1 sq.cm. In the *Glaux* low community *G. maritima* is the commonest species, but only becomes constant on areas of 25 sq.cm., and in the *Honkenya* shingle community the commonest species is *H. peploides*, and the area on which it first becomes constant is 625 sq.cm. It is thus possible to measure to some extent the relative frequency of occurrence of species by noting the size of the sample area on which they first become constant.

It has also been assumed that rare species are those which occur once only in twenty samples of 64 sq.m., together with those which grow in the community but are not represented in the samples taken at random. Hence it has been possible to draw up a summary of the species of common, rare and intermediate occurrence for eight communities. This is given in Table 12. It will be seen that these figures support Preston's contention that the common and rare species in a population are less numerous than those represented by individuals of intermediate occurrence.

Table 12. *The commonness and rarity of species*

Community	Total species	Smallest area of constancy (sq.cm.)	'Common' species		'Rare' species		'Intermediate' species	
			No.	Percentage	No.	Percentage	No.	Percentage
Honkenya shingle	22	625	1	4.54	5	22.7	16	72.76
Eriophorum bog	22	625	2	9.09	4	18.18	16	72.73
Psamma dune	40	625	2	5.0	8	20.0	30	75.0
Glaux low	36	25	1	2.77	5	14.0	30	82.23
Salicornia marsh	12	1	1	8.33	1	8.33	10	83.34
Nardus grassland	38	625	4	10.5	± 2	± 5.25	± 32	± 84.25
Festuca chalk grassland (Pitstone)	67	25	1	1.5	± 11	16.4	± 55	± 82.1
Limonium marsh	15	25	1	6.66	1	6.66	13	86.68

In the herbaceous communities under discussion the commonest species was, in practically every case, the species which was chosen subjectively as the dominant species of the community. This is not unexpected as the communities were chosen for their uniformity of life form. Hence it is probable that the areas for common species in Table 12 indicate the size of sample which would be necessary to check the density of the dominant species and so define the limits of the community more accurately. In the *Honkenya*, *Psamma*, *Eriophorum* and *Nardus* communities the dominant should occur in at least 95% of the samples of 625 sq.cm. For the *Glaux*, *Limonium* and *Festuca* communities 25 sq.cm. would be the size of the test samples, and for the *Salicornia* marsh an area of 1 sq.cm. would be sufficient. Where the frequency of the species showed a significant deviation for quadrats of the specified size, it is probable that the limits of the community had been exceeded and that there was a significant change in the habitat factors.

SUMMARY

1. Data for the frequency of occurrence of the species in quadrats of different sizes for ten herbaceous communities are presented as a preliminary to a statistical analysis which will be directed towards defining the specific character of these communities in quantitative terms.

2. It is assumed that the plant community occupies a finite area and consists of a finite number of species, both of which are determined by the dominant species in conjunction with the climatic, topographic and edaphic factors.

3. A new form of folding frame for a multiple quadrat which facilitates sampling is described.

4. A method is suggested for estimating the commonness and rarity of species and it is noted that for the plant populations under consideration the common and rare species are less numerous than the species which are represented by individuals of intermediate density.

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THE SPECIFIC CHARACTER OF PLANT COMMUNITIES

II. A QUANTITATIVE APPROACH

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(With eight Figures in the Text)

In the preceding paper of this series lists of species, together with their frequency of occurrence in samples of different sizes for ten herbaceous communities, were recorded. It is now suggested that in each of these communities a definite 'pattern' of species may be discerned, and it is proposed to show here how this pattern may be defined and used for the quantitative description and comparison of plant communities.

THE PATTERN OF THE COMMUNITY

In sampling plant communities ecologists are aware that there is a constant repetition of some species with an intermingling of other species which may or may not always be present. That is to say, each community may have its own particular 'pattern' of species. Now it was assumed in the previous paper that the community covers a finite area and contains a finite number of species, and that these two constants are more or less determined by the growth and activity of the dominant species. If this be true then the area on which an average of half the total number of species occurs is also a finite character of the community. It is considered that this area may be used to define the pattern of the community, since in any sample of this size the common species will always be present, whilst in addition there will be a number of species of intermediate and rare occurrence, the combination of which will vary from sample to sample according to the nature of the community and the distribution of the species in it. For convenience this area, or unit of the pattern, will be referred to in future as the 50% *area*, and it will be shown later that it is a function of the rate of increase of species over the area.

It is also possible to associate this pattern with the degree of cover, since, if there is a high degree of cover formed by a few plants of common occurrence, the 50% *area* will be small. If, on the other hand, there is very sparse cover by a number of species of intermediate or rare occurrence then the pattern will be represented by a large area, the species being so scattered that it would require a large sample to contain on an average half their total number.

In natural communities the possible combinations of species, in relation to the amount of ground they cover, are considerably greater than the two simple examples given above, and it has been found necessary to note in addition the average number of species per sq.cm. This quantity will be referred to in future as the *specific density*. It may approximate to the density of individuals, or number of individuals per unit area, if the unit of area is sufficiently small in relation to the plant size, as is the case of 1 sq.cm. in relation to the size of herbaceous angiosperm plants.

THE PATTERN IN SOME HERBACEOUS COMMUNITIES

The average number of species per unit area for ten different communities is given in Table 1. Knowing also the total number of species in the community, we may illustrate the increase of species per unit area with increase of the unit of area under consideration by plotting the average number of species per quadrat against the logarithm of the area of the quadrat. This has been done in Figs. 1-5, and from these graphs an approximation to the 50% area (x_{50}) has been obtained.

Table 1. *Observed and calculated values for the average number of species per unit area*

Community	Total species	x_{50} (sq.m.)	k	Average no. of species per unit area							
				Sq.cm.				Sq.m.			
				1	25	625	2500	1	4	16	64
Salicornia marsh	12	—	—	2.15	2.55	3.35	4.05	4.90	5.40	6.80	8.10
		1.5623	0.1319	2.15	2.61	4.26	4.78	5.28	5.86	6.41	6.95
Limonium marsh	15	—	—	1.70	5.65	9.05	10.55	11.25	11.85	12.20	12.40
		0.0159	0.4061	1.70	4.79	9.45	11.29	12.65	13.56	14.15	14.50
Honkenya shingle	22	—	—	0.30	0.85	1.30	2.10	2.80	4.15	6.30	7.85
		500.0	0.2775	0.30	0.72	1.67	1.97	3.33	4.56	6.11	7.94
Carex dune	22	—	—	—	4.20	6.80	7.95	9.40	—	—	—
		3.5481	0.2006	—	4.20	6.76	8.12	9.61	—	—	—
Glaux low	36	—	—	1.65	4.50	7.80	9.25	10.85	12.25	15.80	20.80
		28.1840	0.2419	1.65	3.40	6.40	8.67	11.10	13.82	16.75	19.74
Psamma dune	40	—	—	1.20	3.15	7.75	10.70	13.20	14.30	18.10	21.55
		19.9530	0.2848	1.20	2.75	6.26	8.62	12.00	15.25	18.86	22.68
Eriophorum bog	22	—	—	0.85	1.60	3.60	4.90	6.00	7.55	8.50	10.60
		79.4330	0.2322	0.85	1.60	3.41	4.47	5.77	7.26	8.93	10.70
Nardus grassland	38	—	—	2.55	5.50	11.60	14.70	19.45	—	—	—
		0.8913	0.2894	2.55	5.84	12.00	15.49	19.31	—	—	—
Festuca chalk grassland (Bledlow)	51	—	—	—	8.30	15.35	19.60	23.55	—	—	—
		1.5850	0.2532	—	8.30	15.40	19.75	23.90	—	—	—
Festuca chalk grassland (Pitstone)	67	—	—	2.40	10.45	23.80	29.90	35.00	—	—	—
		0.6310	0.3762	2.40	7.39	19.71	27.61	36.40	—	—	—

It may be noted, in passing, that if the area were to be plotted on a simple scale the curves obtained would be similar in shape to those given for the increase of species over the area by Du Rietz *et al.* (1920), Cain (1938) and many other workers. It has been found, however, that the logarithmic scale is more satisfactory, as it gives an adequate representation of what happens on very large as well as on very small areas.

In a natural community such as the *Salicornia* marsh, which is inundated by all except the lowest tides, the percentage area covered is high and the average specific density is also high (2.15), but the total number of species is only twelve. The pattern of the community is made up of two species, *S. stricta* and *Pelvetia canaliculata*, each with numerous individuals covering the greater part of the area, whilst the remaining species are represented by widely scattered individuals. The 50% area is 1.5623 sq.m., and is rather larger than might be expected for what at first sight appears to be a very uniform community (Pl. 6, phot. 1, Part I). The pattern is thus that of two densely and constantly distributed species with a variety of scattered species.

A comparison can be made with the *Limonium* marsh, which is inundated only by the highest tides. It has a total of fifteen species, nine of which are similar to those found on the *Salicornia* marsh. On areas of 625 sq.cm. no less than six species will always or nearly

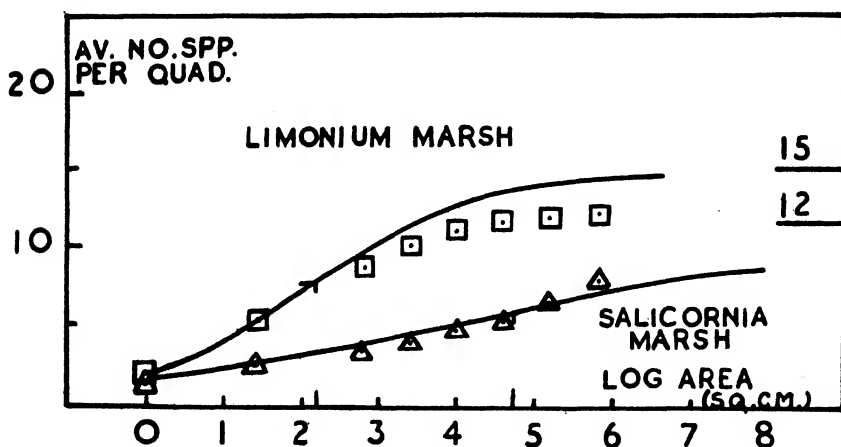


Fig. 1. Species-area curve for *Salicornia* marsh ($\log x_{50} = 4.75$; $x_{50} = 1.56$ sq.m.) and for *Limonium* marsh ($\log x_{50} = 2.2$; $x_{50} = 0.0158$ sq.m.). In this and in subsequent species-area curves the continuous line represents the curve fitted according to the method given in the text. The figures on the right-hand side of the graph give the total number of species in the community. Key to quadrat sizes:

Area of quadrat		Area of quadrat	
Log	Sq.cm.	Log	Sq.m.
0	1	4.0	1
1.39	25	4.6	4
2.79	625	5.2	16
3.39	2500	5.8	64

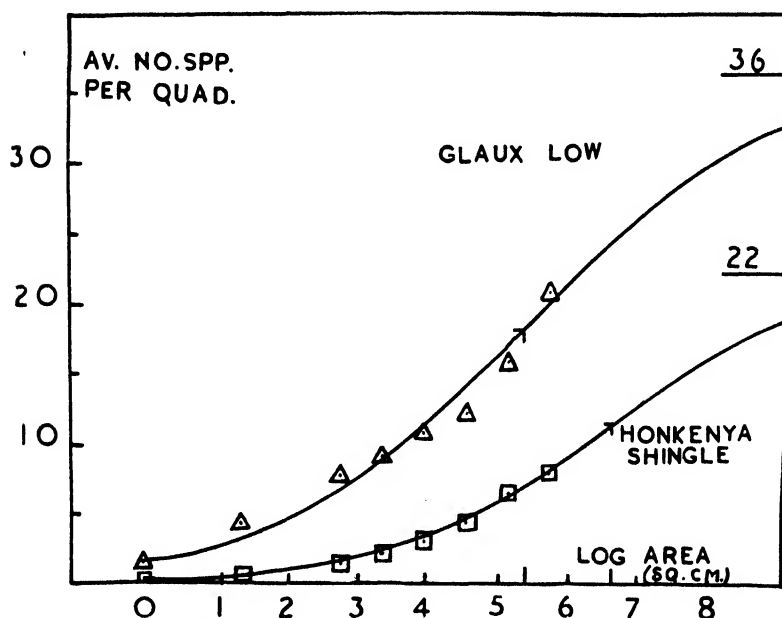


Fig. 2. Species-area curve for *Honkenya* shingle ($\log x_{50} = 6.7$; $x_{50} = 500$ sq.m.), and for *Glaux* low ($\log x_{50} = 5.45$; $x_{50} = 28.14$ sq.m.).

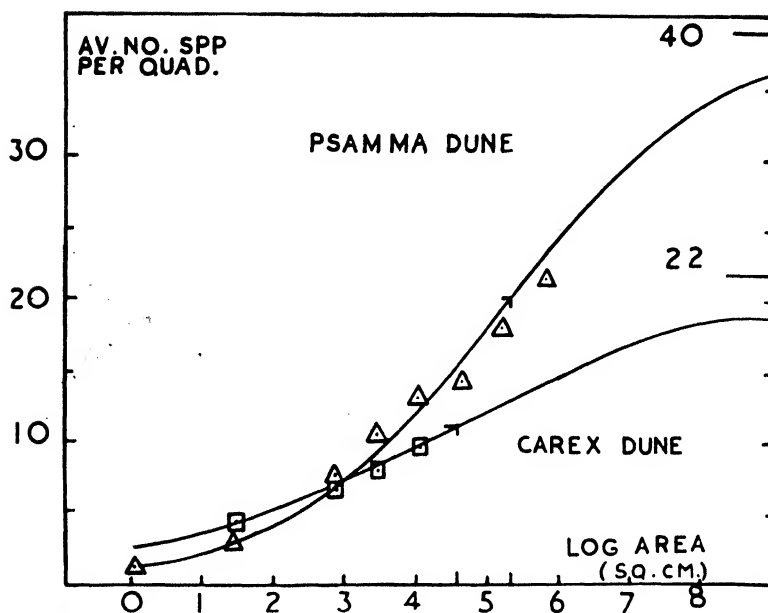


Fig. 3. Species-area curve for *Carex* dune ($\log x_{50}=4.55$; $x_{50}=3.5481$ sq.m.), and for *Psamma* dune ($\log x_{50}=5.3$; $x_{50}=19.953$ sq.m.).

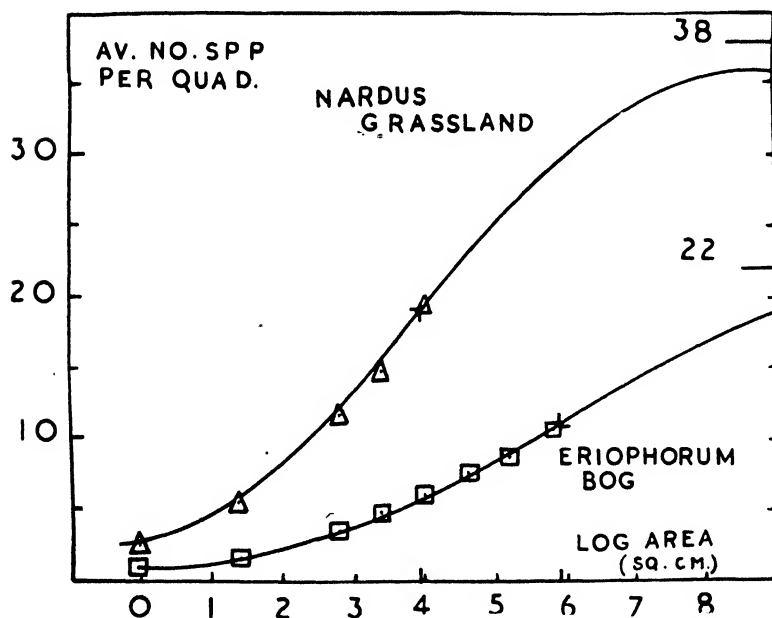


Fig. 4. Species-area curve for *Eriophorum* bog ($\log x_{50}=5.9$; $x_{50}=79.43$ sq.m.), and for *Nardus* grassland ($\log x_{50}=3.95$; $x_{50}=0.8913$ sq.m.).

always be found (Table 2, Part I), and the 50% area is consequently very small (0.0158 sq.m.). The pattern here is that of a closely packed but constant variety of species.

In the case of the *Honkenya* shingle, where less than one-sixth of the area is covered, there is a total of twenty-two species, but only *H. peploides* is at all conspicuous, covering about one-eighth of the area. The 50% area is very large (about 500 sq.m.) and the pattern

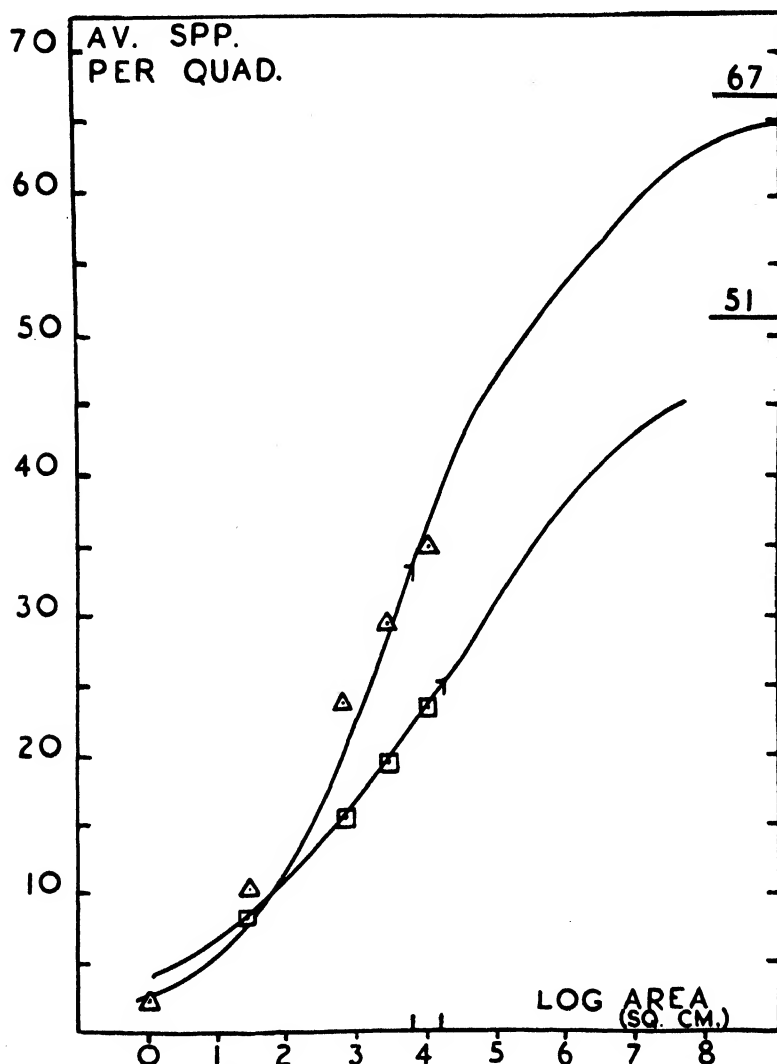


Fig. 5. Species-area curve for *Festuca* chalk grasslands. Bledlow: *Helianthemum-Thymus* ($\log x_{50} = 4.2$; $x_{50} = 1.585$ sq.m.; total species 51). Pitstone: *Linum-Briza-Koeleria* ($\log x_{50} = 3.8$; $x_{50} = 0.6310$ sq.m.; total species 67).

is that of a very large group with one species of medium or low density and a comparatively large number of species represented by very few, widely scattered individuals, a large proportion of the area being covered by pebbles.

The *Eriophorum* bog also has rather a large 50% area, about 80 sq.m., and the pattern here is of a number of large tussocks of *E. vaginatum*, each almost invariably accompanied

by *Deschampsia flexuosa* and *Webera nutans*, while the remaining species out of a total of twenty-two are for the most part widely scattered. The specific density is low (0.85) because of the size of the *Eriophorum* tussocks and the large number of persistent old sheaths which occupy a considerable portion of the space, and also because the channels between the tussocks are so overshadowed by *Eriophorum* leaves that few species can survive in them. Therefore it is not unreasonable to suggest that the peculiar edaphic conditions of the bog find expression in the small number of species per sq.cm. and the low rate of increase of species over the area.

In the case of the *Psamma* dune there are large tussocks of *Ammophila arenaria*, but the spaces between the smaller tussocks are colonized by a variety of lichens, mosses and angiosperms (Pl. 7, phot. 3, Part I) so that the specific density is higher (1.2) than might be expected from the general appearance of the community. The 50% area is about 20 sq.m. and the pattern is that of a few constantly recurring species of low density accompanied by a variety of scattered species.

For the *Nardus* mountain grassland and the *Festuca* chalk grassland there is complete cover and a very high specific density, 2.55 and 2.4 species per sq.cm. respectively. The total number of species is large, but there are comparatively few very rare species, and it is found that the size of the pattern unit is small, from 0.5 to 1 sq.m., and that it includes a large number of constantly recurring species of intermediate density, and a few rare or occasional species.

Thus the specific density and the 50% area may be said to be important specific characters of the community, because they are functions of the degree of cover, the proportion of common and rare species, the total number of species in the community and the rate of increase of species with increase of area. Together they define in a quantitative way the pattern of the community. Both can be fairly easily obtained by direct observation, but it is absolutely essential that a measuring frame should be employed for determining the area of the samples, particularly for samples of 1 sq.cm.

THE FORM OF THE SPECIES-AREA CURVE

When plotted against the logarithm of the area of the quadrat the average number of species per unit area for the *Limonium* marsh gives an S-shaped curve as shown in Fig. 1. For large areas the number of species tends to become constant, and asymptotic with the total number of species in the community. It is particularly evident in this case as the total number of species is small and the pattern unit is also small. With increase in the total number of species and in the size of the pattern unit, very large sample areas would be necessary before the asymptotic effect would be evident; that it must occur is unquestionable if the community is limited by a finite area and a finite number of species. From the evidence of all the communities there seems little doubt that the species-area curve is S-shaped when the area is plotted on a logarithmic scale.

It is desirable to have some form of equation which will express the relationship between the increase in species with increase in the sample area. Several types of equation have been suggested as, for example, those by Gleason (1925), Pidgeon & Ashby (1940) and Fisher, Corbet & Williams (1943). They generally give a good fit over the central portion of the curve, where the relationship between the average number of species per unit area and the logarithm of the area appears to be more or less linear. However, none of them will give a good estimate of the average number of species on very small or on very large areas,

nor do they take into account that the community is limited by a finite area and by a finite number of species.

The point to be made is that any one of a number of equations might fit the data, but its use is not permissible unless the parameters can be interpreted in accordance with the ecological concepts involved; therefore the discussion is now directed towards an examination of the basic principles which are encountered when a plant community is sampled by the quadrat method.

THE PROPORTIONAL REPRESENTATION OF SPECIES

If a constant number of samples of a plant community are taken with quadrats of different sizes, starting from very small quadrats and proceeding to very large quadrats, the number of samples in which the species '*A*' is present will be very small with small quadrats, but will rapidly increase with quadrat size until all quadrats over a certain size will contain the species. That is to say, the frequency of species '*A*' becomes constant when quadrats over a certain size are used. The rate at which a species becomes constant will depend on the size of the individuals and the number of individuals per unit area.

Considering two species *A* and *B* which are distributed at random, and which are represented by individuals of similar size but in number in proportion to 2:1 respectively, then if *x* is a quadrat of such a size that one, and only one, individual of *A* is always present, and if a 100 samples are taken, the expected frequencies of *A* and *B* will be 100*A* and 50*B*. If the quadrat size is doubled the expected frequencies for a quadrat of 2*x* will be 100*A* and 100*B*.

Similarly, for four species *A*, *B*, *C* and *D*, in which the individuals are distributed at random and are of the same size, but are present in the proportions of 8:4:2:1, the expected frequency distribution for a quadrat of size *x* such that one, and only one, individual of *A* is always present will be:

	Frequency of occurrence				Combined frequency of occurrence	Average frequency of occurrence
	<i>A</i>	<i>B</i>	<i>C</i>	<i>D</i>		
For <i>x</i>	100	50	25	12	187	1.87
For 2 <i>x</i>	100	100	50	25	275	2.75
For 4 <i>x</i>	100	100	100	50	350	3.50
For 8 <i>x</i>	100	100	100	100	400	4.00

The combined frequency for all species will only become constant when all species in the community occur in every sample. This is the total possible frequency, and the rate of change for the combined frequency will be proportional to the product of the combined frequency for any area, and the total frequency less this combined frequency. But the combined frequency is directly proportional to the average frequency or the average number of species per unit area, so the above hypothesis may be reworded as 'the rate of change of the average number of species per unit area is approximately proportional to the product of the average frequency of occurrence per sample area and the average frequency of absence'.

The increment in the average number of species per unit area may therefore be written as

$$\frac{dy}{dx} = k'y(S - y), \quad (1)$$

where *y* is the average frequency of occurrence, or average number of species on an area *x*, *S* is the total number of species in the community, and *k'* is a constant.

The form of the equation is similar to that derived by Brailsford-Robertson (1908) for the quantitative relation between the amount of growth and the time of growth of an individual.

Integrating equation (1) we have

$$\log_e \frac{y}{S-y} = Sk'x + C, \quad (2)$$

where C is a constant of integration. Equation (2) may be written as

$$\log_{10} \frac{y}{S-y} = Skx + C. \quad (3)$$

When the average number of species per unit area is equal to half the total number of species in the community we have

$$y = \frac{1}{2}S \quad \text{and} \quad \log_{10} \frac{y}{S-y} = 0,$$

and $C = -Skx_{50}$, where x_{50} is the area on which $y = \frac{1}{2}S$ species occur. As the area range is very great it is necessary to use a logarithmic scale and equation (3) becomes

$$\log_{10} \frac{y}{S-y} = k (\log x_{10} - \log x_{50}). \quad (4)$$

Knowing S from observation, and having a series of values for y , an estimate for x_{50} can be obtained from the graph of y in relation to $\log x$, and by substituting in equation (4) we can solve for k . This has been done for the ten plant communities under consideration and a value for k found from the smallest-sized quadrat observed. Hence observed and calculated values for y are compared in Table 1 and in Figs. 1-5. It will be seen that there is a good fit in all cases and that the fitted curve is an S-shaped one in which the average number of species on large areas becomes asymptotic with the total number of species in the community. Equation (4) is thus in accordance with the basic principles of the method of sampling, and it also makes use of the 50% area which has already been referred to as an important characteristic of the community; it is therefore worth while to consider the further implications of this equation.

The value of k

The value of k has been calculated for all observed values of x and y , and the average value for each community, together with the average value for all communities, is given in Table 2.

Table 2. *Values for k*

Community	Total species	k for 1 sq.cm.	Average k	Standard deviation
Salicornia	12	0.13195	0.26198	0.13265
Limonium	15	0.4061	0.27570	0.06364
Carex	22	—	0.21032	0.01416
Honkenya	22	0.2775	0.28820	0.01686
Glaux	36	0.2419	0.28637	0.08428
Psamma	40	0.28484	0.32881	0.21041
Eriophorum	22	0.2322	0.24757	0.03885
Nardus	38	0.2894	0.33218	0.05697
Festuca (Bledlow)	51	—	0.27521	0.03364
Festuca (Pitstone)	67	0.3762	0.27202	0.06309
Average			0.27782	0.03392

Differences in the value of k chiefly affect the expected values of the average number of species on very small and very large quadrats, for it will be seen from Table 1 and Figs. 1-5 that the agreement for observed and calculated values of y over the middle portion of the curve is very good when the value of k is derived from the average number of species on 1 sq.cm. The average value for all communities, $k=0.27782$, would also give a good approximation over the central portion of the curve, but in some cases would show a noticeable error in the estimation of the average number of species on very small and possibly on very large areas. This error would be greatest in the *Salicornia*, *Limonium*, *Nardus* and *Festuca* communities, where the cover is very dense and the number of species per sq.cm. is high. Further investigation of the theoretical value of k is needed, but for the purpose of the present discussion it is sufficient to conclude that the hypothesis of combined frequencies, as expressed by equation (4), shows no significant departure from observed facts, and that the equation gives a close approximation for the average number of species per unit area provided the initial increment, or average number of species on 1 sq.cm., is used in the calculation of the constant of the equation.

The relation between x_{50} and y_0

It appears that x_{50} , the area on which an average of half the total number of species in the community occurs, and y_0 , the average number of species on 1 sq.cm., are both important characteristics of the community, and that x_{50} varies with y_0 , or $x_{50}=f(y_0)$. Considering the reciprocal of y_0 we have $1/y_0=x_0$, which is the area, in square centimetres, on which an average of only one species would be expected. The values for $1/y_0$ for eight communities are given in Table 3 and the relationship between $1/y_0$ and x_{50} is shown graphically in Fig. 6.

Table 3. *Relation between $1/y_0$ and x_{50}*

Community	$\frac{1}{2}S$	y_0	$1/y_0$	$\log x_0$	$\log x_{50}$
Limonium marsh	7.5	1.70	0.588	1.769	2.2
Nardus grassland	19.0	2.55	0.392	1.593	3.95
Festuca chalk grassland	33.5	2.40	0.416	1.619	3.8
Salicornia	6.0	2.15	0.465	1.667	4.75
Glaux low	18.0	1.65	0.606	1.782	5.45
Psamma dune	20.0	1.20	0.833	1.920	5.3
Eriophorum bog	11.0	0.85	1.177	0.070	5.9
Honkenya shingle	11.0	0.30	3.333	0.522	6.7

It will be seen from Fig. 6 that the points appear to lie on a parabola the vertex of which is given approximately by $\log x_{50}=4.75$ and $1/y_0=0.38$.

The actual curve of the parabola is purely hypothetical, but it at once draws attention to the fact that the whole problem of the distribution of species in plant communities hinges on the amount of space available for a plant, and therefore it is this aspect of the problem which will be discussed next.

THE SPATIAL LIMITS IN PLANT COMMUNITIES

Considering the position of the various communities in Fig. 6 we see that the small pattern communities, that is those having a 50% area of 1 sq.m. or less, lie to the left of the figure, and the large pattern communities with a 50% area of more than 1 sq.m., lie to the right of the figure. Communities with sparse cover occur in the upper two-thirds of the

figure and have an average area per species of 1.5 sq.cm. or more, while communities of medium to complete cover with an average area per species of less than 1.5 sq.cm. occur in the lower third of the figure.

Now according to the size of the individuals which make up the community there must be some limit to the average number of species which can occur in an area of 1 sq.cm.; therefore the lower limit of $1/y_0$ will depend on the average size of the plants in the community. It has already been pointed out that the communities were chosen for their uniformity of life form, being composed chiefly of herbaceous angiosperms. By observation we find that in communities with complete cover, such as the *Nardus* grassland and *Festuca* grassland, the average number of species per sq.cm. is 2.55 and 2.4

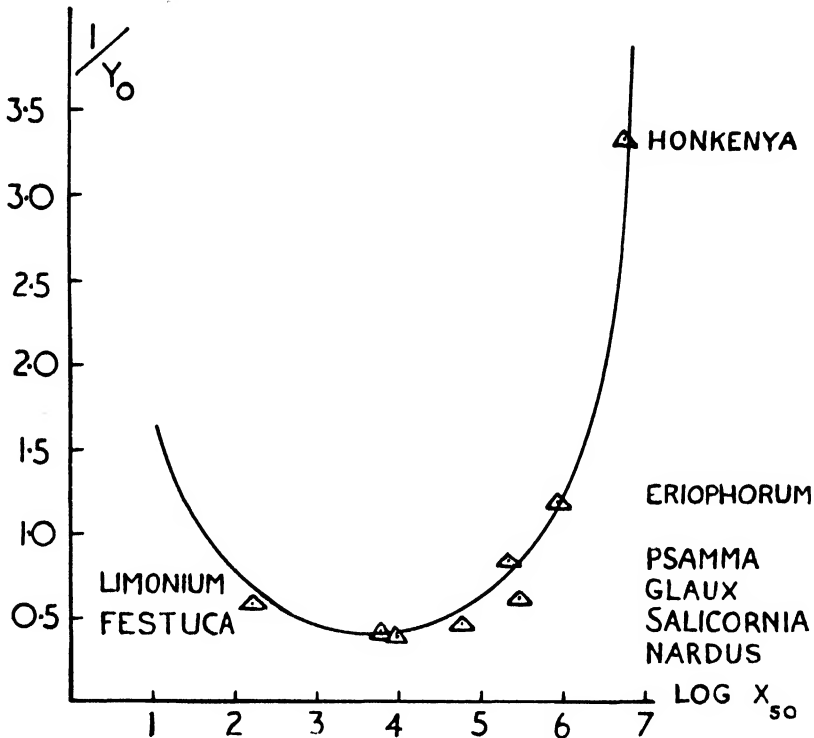


Fig. 6. Relation between the 50% area (x_{50}) and the specific density or average number of species per sq.cm. (y_0) for eight communities (cf. Table 5).

respectively. Therefore it is not unreasonable to suppose that for herbaceous angiosperm communities the average number of species per sq.cm. is unlikely to be greater than 2.6, which puts the limiting value of $1/y_0$ at 0.38 sq.cm. per species, and $\log x_0 = 1.584$.

It has been shown that the species-area curve is S-shaped when plotted on a logarithmic base and can be approximated by the equation

$$\log_{10} \frac{y}{S-y} = k(\log_{10} x - \log_{10} x_{50}).$$

It can also be shown that the maximum increment for this equation would occur when $y = \frac{1}{2}S$. We may, therefore, conclude that the maximum increment per unit area occurs when the sample area includes an average of half the total species in the community, and

any further increase in sample area will be accompanied by a decrease in the increment per unit area. This is made clear in Fig. 8*b* and will be referred to again in the concluding part of the discussion.

Now the increment per sq.cm. cannot exceed the average number of species per sq.cm., otherwise we would suspect that we had got beyond the limits of the community. Therefore the maximum increment per sq.cm. at x_{50} cannot exceed the initial value of y_0 .

This increment can be written as $dy/dx = \tan \theta$, where θ is the angle of increment. The value of θ can be obtained for each known limit of y_0 , and for the herbaceous angiosperm communities under consideration the upper limit is given by $\tan \theta = 2.6$ and $\theta = 69^\circ$ approximately.

Conversely, a lower limit for y_0 can be found by supposing that a community is not likely to exist with a total of less than two species and an angle of increment less than 2° . Then $\tan \theta = 0.03 = y_0$, and from equation (4), $\log x_{50} = 6.75$ when $k = 0.27782$.

At present it is not necessary to emphasize the exact dimensions of the limits but rather to point out where ecological requirements and mathematical probability coincide.

PLANT COMMUNITIES IN RELATION TO A PARTICULAR GEOGRAPHICAL AREA

Having had the opportunity of studying plant communities in regions with such widely different climatic and edaphic conditions as South Africa and the British Isles, my impression is that in South Africa plant communities are characterized by a much greater variety of species but less continuous cover than they are in the British Isles. It may be possible, therefore, that the pattern of the community can be used to distinguish between communities of different geographical areas, for the pattern has been defined in terms of the total area, which is related to topography; the total number of species and their variety, which are partly influenced by geography; and the specific density which is dependent on climate and soil.

In order to illustrate this point I shall attempt to show how the probable ecological limits of herbaceous communities in the British Isles could be defined.

Thus, for communities which contain the greatest number of species, such as chalk grasslands, the total number of species found has not been as much as eighty and it seems unlikely that communities with more than a hundred species exist. At the other extreme when the flora is extremely poor, as it is in many maritime situations or on mountain tops in northern latitudes, a community of less than two species is also unlikely to exist. It is probable too that the total area of communities of extreme habitat will not be greater than three or four acres because of the variations in topography as, for example, along coast-lines or at great elevations. With these rough approximations attention can now be drawn to Fig. 7, and it can be suggested why certain portions of the graph can be eliminated.

The portion to the right of $\log x_{50} = 7$ will probably not contain any observations because when the angle of increment is very small the total area of the community would have to be several acres if it contained more than two species, and this is inconsistent with ecological conditions. As the angle of increment increases the total number of species in the community becomes greater and the position of the 50% area moves to the left of the log scale, so that for the maximum increment of 2.6 species per sq.cm. and a total of a hundred species the expected value of $\log x_{50}$ is 5.8. Beyond this point the total number of species decreases rapidly for all values of $1/y_0$, while on the extreme left of the scale the area up to

$\log x_{50} = 1.46$ is eliminated by the mathematical limits of x_0 , the area on which an average of only one species occurs. We can also assume that communities with $\frac{1}{2}S = 2y_0$ are unlikely to occur, and by substituting these limiting values of S and y_0 in equation (4), expected values for $\log x_{50}$, when $k = 0.27782$, can be found. In this way we get the various limits given in Table 4 and the possibilities they eliminate are shown diagrammatically in Fig. 7.

Table 4. *Limiting values for herbaceous angiosperm communities in the British Isles*

y_0	$\tan \theta$	θ	$1/y_0 = x_0$	$\log x_0$	S	$\log x_{50}$
2.6	2.6	69°	0.384	1.584	100	5.8
2.6	2.6	69°	0.384	1.584	10.4	1.77
0.66	0.66	33°	1.5	0.176	100	8.0
0.66	0.66	33°	1.5	0.176	3	2.0
0.33	0.33	18°	3.0	0.477	2	2.67
0.034	0.034	2°	29.4	1.468	2	6.75

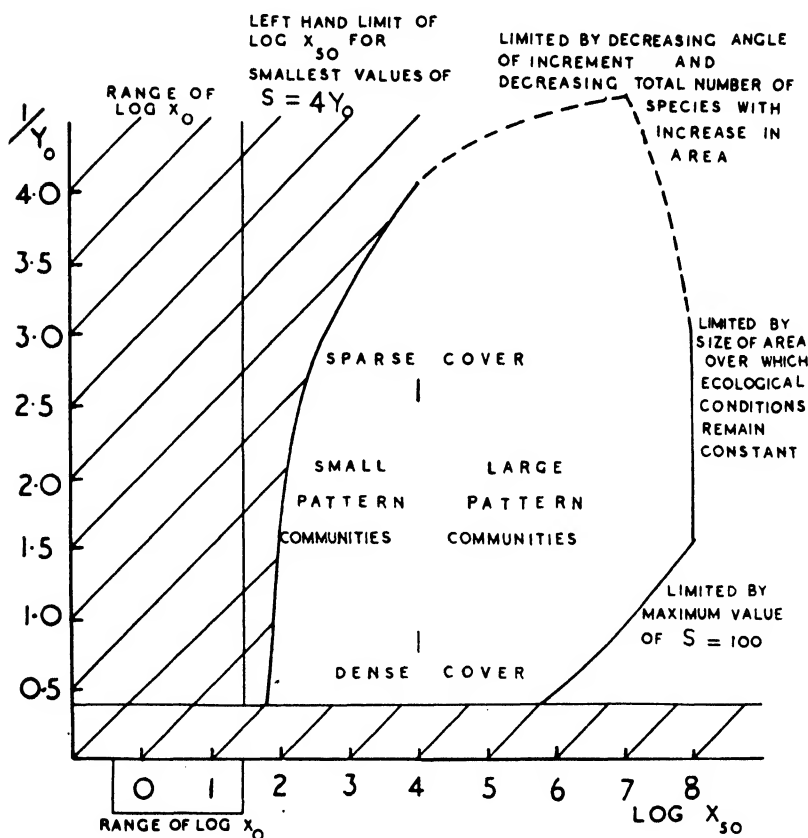


Fig. 7. Diagram to illustrate the relationship between the pattern and the degree of cover in herbaceous communities, and the extent to which they are limited by (i) the total area of the community, (ii) the total number of species (S), (iii) the rate of increase of species with increase in area as given by the 50% area (x_{50}), and (iv) the average number of species per sq.cm. (y_0). Cf. Table 4.

A closer study on these lines of communities in the British Isles would lead to a more exact definition of the limits, and it is conceivable that they would differ significantly from the limits of communities in a semi-arid region, say, where the total area might

be more extensive, the variety of species more considerable and the percentage cover far less.

CONCLUSION

In conclusion I find that a quantitative estimation of the specific character of the community depends largely on the interpretation of the species-area curve. If the community can be defined by a finite area and a finite number of species, then increase of the sampling area must be accompanied by an increase in the average number of species per unit area and this will become asymptotic with the total number of species in the community. The results may be shown graphically by plotting the average number of species per unit area either against the area or the logarithm of the area, and the increment per unit area can be plotted on the same scale. Diagrams of the shapes of the curves given by these two methods, together with their respective increment curves, are given in Fig. 8*a, b*. Reference

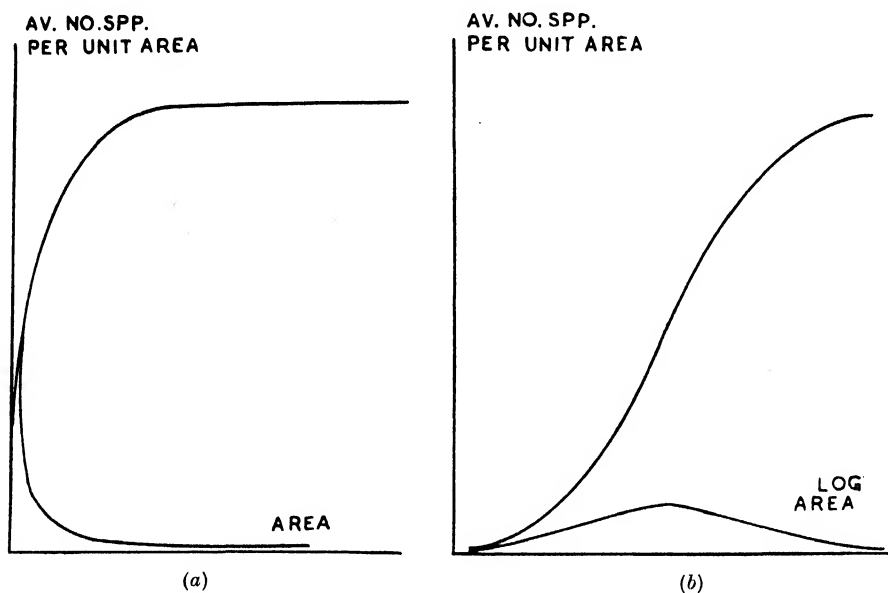


Fig. 8*a* and *b*. Diagrams to show the distribution of the increment when the average number of species per quadrat is plotted against (*a*) the area of the quadrat, and (*b*) the logarithm of the area of the quadrat. In both figures the upper curve is the species-area curve and the lower one is the corresponding curve for the distribution of the increment.

has already been made to the equations formulated by previous workers to express the relationship between the increase in the number of species and the increase in sample area. These equations are either linear, having a constant increment, or are based on the logarithmic series, for which it is said that doubling the sample size adds $\alpha \log_e 2$ species to the original number (Williams, 1947). It will be seen, therefore, that both forms of increment are inconsistent with the rate of increase for the species-area curve, for whether it is plotted on a simple scale or on a logarithmic scale, its increment curve reaches a maximum at a certain point and then decreases and becomes infinitesimally small.

The platykurtic shape of the increment curve when results are plotted on a logarithmic scale at once suggests that the S-shaped species-area curve is a true sigmoid curve in which the increment is normally distributed. To test this supposition two methods were used. The observed readings for the average number of species per unit area were converted to

percentages of the total frequency and then transformed either in terms of the normal equivalent deviate (Pearson, 1945), or in terms of Finney's tables for probit analysis (Finney, 1947). If the observed points fall on a true sigmoid curve then the transformation, in both cases, will give a straight line. The results for both methods were essentially the same. For all communities except the *Limonium* marsh and *Salicornia* marsh, where the initial increment is high in proportion to the total number of species, the transformations gave a straight line. However, it has not been possible to find an expression for the normal sigmoid curve which could be interpreted in accordance with the requirements of the problem, and so the approximation given by equation (4) is suggested.

SUMMARY

1. The 'pattern' of the community is defined by the 50% area (x_{50}), which is the area on which an average of half the total number of species in the community occur, and by the specific density (y_0), which is the average number of species on 1 sq.cm.

2. It is shown that if the average number of species per unit area is plotted against the logarithm of the area then, with increase of the unit of area under consideration, an S-shaped curve is obtained for a community which consists of a finite number of species and a finite area.

3. It is suggested that the relationship between the increase of species with increase of area can be expressed by the equation

$$\log_{10} \frac{y}{S-y} = k (\log_{10} x - \log_{10} x_{50}),$$

where y is the average number of species on an area x , S is the total number of species in the community and k is a constant.

4. The point of maximum increment of the curve given by this equation occurs when $y = \frac{1}{2}S$, and hence it is concluded that the increment in the number of species per sq.cm. is greatest at the 50% level and that it cannot exceed the value for the average number of species per sq.cm. (y_0), which is taken as the basic increment of the community.

5. The parameters y_0 and x_{50} are regarded as important characteristics of the community, as they are respectively functions of the degree of cover and rate of increase of species over the area, both of which express the reaction of the species to the climatic and edaphic factors governing the community.

6. It is shown that plant communities can be divided into those with a large pattern unit and those with a small pattern unit. This leads to the consideration of the spatial relations in natural communities and a suggestion is made as to how the probable limits for herbaceous angiosperm communities in the British Isles may be defined.

The author's ideas and opinions on these problems were formed during the tenure of the Quain Studentship at University College, London. She wishes to thank Prof. W. H. Pearsall, F.R.S., whose kindly comments and interest throughout the whole work were a source of great inspiration and encouragement.

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THE UNIVERSAL FEATURES OF ZONATION BETWEEN TIDE-MARKS ON ROCKY COASTS

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(With Plate 8 and four Figures in the Text)

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INTRODUCTION

So much has already been discovered about life between tide-marks that it has become difficult to see the wood for the trees. Yet despite the host of publications dealing with intertidal life, the field untouched is so vast that our knowledge of the natural laws which control intertidal affairs is still elementary. For these reasons we must examine intertidal arrangements, where possible, on a broad scale as well as intensively.

Until recently there has been a stronger tendency to study the problems of tidal biology in great detail on a small scale than in less detail on a large one. This has resulted in many accounts of the natural history of individual plant and animal species, and in numerous descriptions of the occurrence of plants, animals (or both) in small areas varying in size from square yards, individual rock-pools or narrow traverses to short stretches of coastline, estuaries and similar areas. The general examination of long stretches of coast, or of the coastlines of whole countries, has lagged far behind the more detailed studies, and there have been few examples of it. We have, it is true, such surveys as those of Fischer-Piette on the European coasts, of Ricketts on the Pacific coast of North America, and of the present authors and their collaborators in South Africa; but the list is not a long one. Recent progress in intertidal studies has been ably summarized by Fischer-Piette (1940), and the volume in which his paper appears represents, as a whole, an important contribution to the subject.

At the present time there is evidence of a tendency to undertake the examination of long coastlines more readily than before, and this is of course facilitated by car and plane travel, and by the construction of roads in many places which were previously inaccessible. An example of such work is the survey, by Dakin and his assistants, of 1000 miles of coastline in New South Wales, the results of which were published in 1948. A series by R. G. Evans on parts of the British coast is at present appearing, and while this deals with much shorter stretches, its point of view is a broad one, looking towards an eventual general account of the British coasts. There is similar work now progressing in several parts of the

world. Another welcome development has been an increasing willingness to include both the plants and the animals in marine ecological studies, which have suffered too often in the past from the omission of one or other of these elements which are, in nature, so inextricably interrelated that no balanced account can be achieved without both.

During the preparation of a book on the intertidal fauna and flora of the world, we have come to certain tentative conclusions about intertidal zonation which we think it advisable to put forward without further delay. As it may well be 5 or 10 years before we can present these in full detail with all the supporting evidence, we venture to state them in outline now, in the hope that they will be of assistance to those following similar lines of work during the coming decade.

This paper, though short, is based on first-hand experience of coastal areas in several parts of the world, extending over more than 30 years. The regions studied are situated in the following areas:

- (1) England, Scotland and Wales.
- (2) South Africa between the mouth of the Orange River in the west and the border of Portuguese East Africa in the east.
- (3) The Indian Ocean and Red Sea—Mauritius, Mombasa, Mozambique, Port Sudan.
- (4) The Great Barrier Reef of Australia.
- (5) The coasts of North America between Prince Edward Island and Key West on the Atlantic side, and between Vancouver Island and San Diego on the Pacific side.

ZONATION BETWEEN TIDE-MARKS

I. *The standard zonation* (Figs. 1–3)

Authors describing the distribution of plants and animals between tide-marks, in different parts of the world, have usually found that the tidal belt is subdivided into strips or zones, one above the other, each of them characterized by distinctive features of its own. The number of these zones varies from shore to shore, and each author has adopted for them whatever system of nomenclature seemed to be appropriate to the particular place which he studied. The result is that various local names exist, but none has so far been invented which is of universal application; nor has there been any serious attempt to compare the parts of the world with one another. It is our purpose in the following paragraphs to introduce a system which we believe *may* prove to be of universal application.

It may well be asked, is there any reason to suppose that any universal type of zonation exists? Should we not rather suppose that, in view of the numerous known variations of tidal behaviour, there must be a corresponding diversity of zonations showing little in common? Let it be stated at once that nobody can give a final answer to these questions at the present time. There is information available upon which answers in both senses could be devised, and an affirmative to the second one might be developed, for instance, from an important recent paper by Doty (1946) or from unpublished observations of our own in North America. We believe, however, that it is at least true that zonation has certain features which are very widespread, frequently recurrent, and perhaps even universal in occurrence. It is our object to indicate these features and to suggest a terminology suited to them, because we feel that it will probably contribute towards clarity of thinking, in the future development of intertidal studies, if a general system is introduced, even if it is experimental at the present stage. If the same system could be adopted by

everyone, it would make the accounts published in one part of the world much more intelligible to workers in other parts; and if the features which tend to be universal are pointed out, they can be looked for as new coasts are described, until we have a body of information extensive enough for a final decision. Even should the final decision be against the applicability of a general system, it cannot be reached until the possible system has been identified, defined and tested.

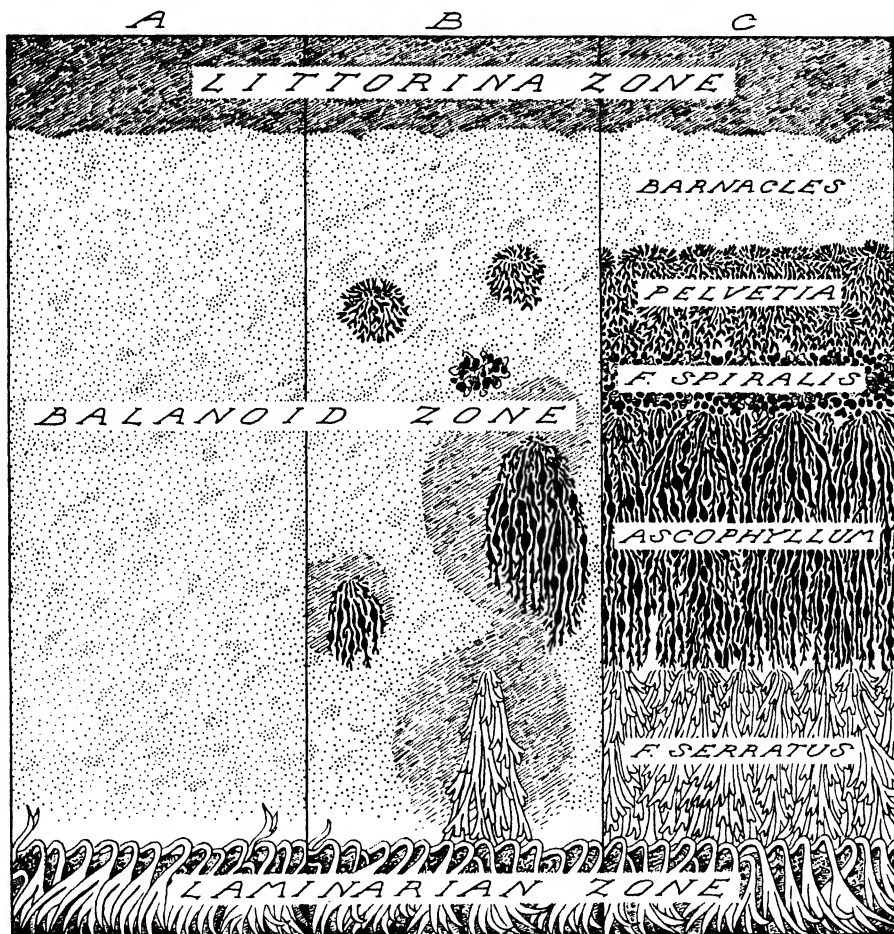


Fig. 1. A diagram illustrating three of the possible types of zonation met with on the British coasts (e.g. on steep rock-faces in Argyllshire). In column *A* the three widespread zones described in the text (Littorina zone, Balanoid zone and sublittoral fringe, represented here by a Laminarian zone) are alone developed. In column *B* the Balanoid zone is colonized by patches of brown algae at different levels (the lower ones surrounded by areas of bare rock more or less free from barnacles). In column *C*, a full series of Fucoid zones is superimposed on the Balanoid zone, overshadowing the barnacles. (In this diagram only part of the width of the Littorina and Laminarian zones is included. The relative widths of the other zones are accurate for the places chosen. For column *C* a locality without *Fucus vesiculosus* or *Porphyra* was selected.) Reproduced by courtesy of the Linnean Society.

We first developed the idea that zonation may have features of widespread occurrence during our survey work in South Africa (1931-40). This conception was referred to in the *Journal of the Linnean Society* (Zoology, vol. 40, 1939, pp. 506-10), where a short and

preliminary comparison was made between the zones recognizable in South Africa and those of coral reefs on the one hand, and of British coasts on the other. It was concluded that, so far as the available evidence permitted us to judge, there are three zones on the shore which are likely to be of widespread occurrence, though undergoing numerous local modifications. Our more recent work in America (1947-8) has strengthened this impression. These zones are, from above downwards:

(1) *The Littorina zone.* This is an arid zone subject to transitional conditions between land and sea, affected by spray in suspension, but wetted by the waves only in heavy weather or at the higher spring tides, when at least its lower parts become washed or submerged. The number of species inhabiting the zone is small, and includes snails adapted to arid conditions and belonging to the genus *Littorina* and to related genera, or to genera including similarly adapted species. The surface of the rock in the Littorina zone or its lower part is commonly blackened by encrusting Myxophyceae and/or lichens of the *Verrucaria maura* type, and this blackening may exist as patches or may form a distinct blackish belt, often overlapping into the zone below.

(2) *The Balanoid zone.* This is the middle part of the shore, the most fully intertidal region, at least part of which is covered and uncovered every day. The inhabitants are more numerous than in the Littorina zone, and typically include numerous balanoid (acorn) barnacles belonging to genera such as *Balanus*, *Chthamalus* and *Tetrachita*. The upper limit of the zone is marked by the cessation of barnacles (in quantity). There is a strong tendency for the zone to become differentiated into two or more subzones. In the upper of these the barnacles tend to be maximal in number and are either the dominant forms or among these; in the lower, they are usually in competition with other sedentary forms, which may overshadow or obliterate them.

(3) *The sublittoral fringe.* This is the lowest part of the shore, uncovered at spring tides and not at neaps, and sometimes, where wave-action is persistently strong, only at the lowest spring tides in calm weather. It supports the fringe of the sublittoral population (i.e. the population of the region which never uncovers at all), is exposed to the air for a relatively small proportion of the time, and in many places rarely if ever dries off. The population is very variable but usually rich. In many cold-temperate regions it consists of a forest of large brown algae (Laminariales, etc.) with an undergrowth of smaller plants and animals among their holdfasts. On coral reefs it commonly contains the upper edge of the rich growth of coral which extends down the reef face below low-water level. In warm-temperate regions it may support (a) a dense covering of simple ascidians (*Pyura*); (b) a dense growth of rather small mixed algae, primarily Rhodophyceae; or (c) other communities. Large brown algae may or may not occur, but if they do, tend to be less strongly developed than in cold-temperate regions. In the sublittoral fringe the encrusting non-jointed calcareous algae of the family Corallinaceae (referred to broadly as 'lithothamnium') tend to encrust all surfaces suited to them, and this encrustation extends above the fringe where it can do so, though usually not forming a continuous growth above the lower Balanoid zone, except in pools, caverns or other special places.

In the foregoing paragraphs, the features of the zones have been indicated very broadly and as they appear when they exist in their most typical form. When dealing with anything as complex and variable as zonation there must be some arbitrary standard regarded as 'typical' with which variations can be compared. We have found, as have many others before us, that this standard is often best displayed on fairly smooth, con-

tinuous rocky slopes, whether steep or gradual, and that on the whole it is best seen where wave-action is neither absolutely maximal nor yet minimal. At the same time there are many intermediate degrees and types of wave-action, and the several zones vary independently, to some extent, in relation to these, so that it does not follow that all the features mentioned as typical are at their best under exactly the same amount of wave-action.

II. *Deviations from the standard* (Figs. 1, 2 and 4)

To what extent are these zones recurrent, and how much do they vary? Their existence can at least be demonstrated on many parts of the coasts of Britain, the Mediterranean, North America (both Atlantic and Pacific sides), South Africa, Australia and Mauritius, and probably in many other areas. The range of variation is very great, but it seems to concern rather the number of subzones present than the broad general features of the primary zones. It must always be remembered that zonation, like everything else on the shore, responds in the most sensitive and immediate manner to the slightest changes in the amount, type and strength of the wave-action to which rocky faces may be exposed; and that a little more shade or a little more sun, a variation in the slope of the rock, and other changes of this kind, will produce their own effects. We must, therefore, expect one zonation where there is shade and quiet, another where there is shade and turmoil, a third in rock-pools, a fourth on open sunny rock-faces exposed to moderate waves, and many others. These variants do not as a rule, however, depart so far from the standard we have chosen to regard as typical, that they cannot readily be related to it. While it cannot be expected that the variations should be fully covered in a paper of this length, the following notes will indicate the type of change to be expected.

(1) *Littorina* zone. This is very often populated by myriads of small snails (species of *Littorina*, *Tectarius*, etc.) and by *Ligias*, and may have no vegetation beyond encrusting microphytes. It varies from this mean in both directions. It may become highly developed and organized, as it does on the Florida keys, where the snails include several species showing a zonation of their own, there is an invasion of flowering plants from above and of small moss-like marine algae from below, and the zone is divided into three well-marked subzones, in which the rock is differently coloured and supports different selections of species. At the other extreme the snails either become very few (at Marineland in northern Florida we found fourteen *Littorina* in 8 days) or disappear. This does not make it impossible to identify the limits of the zone, as these can be recognized either from the distribution of some other animals, or from that of plants. The blackening which has been mentioned above, as occurring in this zone, is a very widespread feature, but it has been noticed more often by botanists than by zoologists or by general workers. There seems to be no constancy about its cause, except that this commonly consists of a blackening film or crust of more or less microphytic Myxophyceae or lichens adapted for life at a particular level. There are Myxophyceae in all the intertidal zones, and also below tide-marks; and there are lichens throughout the tidal belt and above it; but the particular species of these groups which cause the blackening flourish at the levels which we are considering. The lichens are of the kind exemplified by *Verrucaria maura*, *V. symbalana* and *V. striatula*. The Myxophyceae belong to various genera and species, and during our American work about twenty were collected in this zone. The blackening, when present, may be vague and patchy, or it may form a sharply marked and conspicuous band (Pl. 8; Fig. 4). This band may occupy the *Littorina* zone almost exactly, extend somewhat above it or (probably



Fig. 2.

most commonly) occupy its lower part only, often overlapping into the upper Balanoid zone. The discoloration is not *necessarily* due to Myxophyceae and lichens, but can also be caused by small Chlorophyceae and by encrusting Rhodophyceae such as *Hildenbrandia*; and in special places such as the English chalk-cliffs other variations occur. Moreover, while the discoloration has been referred to broadly as a 'blackening', which it commonly is, the tint may vary from blackish towards grey, green, brown and other shades. Some accounts dealing with this vegetation are those of Anand (1937), Berner (1931), Chapman (1946), Cranwell & Moore (1938), du Rietz (1925), Feldmann (1938), Fritsch (1931, 1945), Geitler (1930-2), Ginzberger (1925), Grubb (1936), Johnson & Skutch (1928), Kylin (1937), and Smith (1921).

(2) *Balanoid zone*. Where this is most obviously developed, the barnacles form a dense continuous sheet on the rock, and the majority shows a rather sharp upper limit which forms one of the best landmarks on the shore; individuals usually straggle above this. Sometimes the barnacles continue downwards uninterrupted (though it need not be the same species all the way down) almost to the sublittoral fringe, either fading off gradually or ceasing with a distinct lower limit. Exceptionally they continue below low-water level of springs. More often something interferes with or suppresses them in the lower parts of the zone, and such interference may extend to quite high levels. The competing organisms may be turf-like growths of short algae, a mass of limy polychaet tubes, a sheet of zoanthids or various other sedentary forms; but there are influences other than competition which also tend to reduce the number of barnacles at the lower levels. Quite often there is a sharp line between an upper Balanoid zone, dominated by barnacles and (perhaps) limpets, and a lower one, which may support a patchwork of algal turf, polychaets and other forms competing with the barnacles. In other places no sharp line can be seen, and in yet others there are more subzones than two. There are also regions where the barnacles are reduced in number or even absent over the entire zone, and here the extent of the zone is indicated by other organisms of similar distribution. It should not be supposed that barnacles are necessarily absent from the zones below the Balanoid—this is not so; for instance, the large *Balanus tintinnabulum* often occurs near or even below low water. But the barnacles characteristic of the Balanoid zone are typically intertidal mid-level species, not the same as those lower down; and the population of the sublittoral fringe is not typically dominated by barnacles even where they occur.

(3) *Sublittoral fringe*. Some indication of the variations to be found in this zone has already been given (p. 292). It is usually recognizable, though there are abnormal regions where it departs in many ways from the standard, usually in the direction of

Fig. 2. A diagram comparing the widespread features of zonation with an example which complicates them. A coast is shown on which smooth granite spurs are exposed to considerable wave-action. On the middle spur some of the widespread features are summarized, and the following succession is shown: *A*, supralittoral fringe (= *Littorina* zone), blackened below by Myxophyceae; *B*, midlittoral (= Balanoid) zone, occupied by barnacles above and lithothamnion below; *C*, infralittoral (= sublittoral) fringe, dominated in this case by Laminarians, growing over lithothamnion. On the other spurs (foreground and background) an actual zonation from the Atlantic coast of Nova Scotia is shown. Here the simplicity of the basic plan is complicated by (a) map-like black patches in the supralittoral fringe, consisting of *Codiolum*, *Calothrix* and *Plectonema*; (b) the existence of a strongly developed belt of *Fucus* (mostly *F. vesiculosus* and *F. edentatus* in this example) occupying a large part of the midlittoral zone and overgrowing all but the uppermost barnacles; and (c) a distinct belt of *Chondrus crispus*, overgrowing the lower part of the midlittoral zone, and largely obliterating the belt of lithothamnion which, on the middle spur, extends above the Laminarians.

a reduction of the population (including a reduction or suppression of the lithothamnia) connected with some special local feature such as, for instance, the wide flats laden with calcareous sediment which occur at this level along the Florida keys. Where well developed, on the other hand, the fringe may include subzones, as in New South Wales, where a *Pyura* belt occurs above a kelp zone (Dakin, Bennett & Pope, 1948).

(4) *Other zones.* The complexities of intertidal zonation are due, not only to variations in the three basic zones, but also to the introduction into the simple basic pattern of additional zones, both in particular parts of the world and under certain combinations of conditions. In Britain, for instance, zonation was long described in terms of the series of seaweeds which frequently form bands along the shore, including the conspicuous brown *Pelvetia canaliculata*, *Fucus spiralis*, *F. vesiculosus*, *F. serratus* and *Ascophyllum nodosum*. It has now been realized (Stephenson, 1939, p. 509; Evans, 1947*a*, p. 283, etc.; 1947*b*, p. 190) that these Furoid zones are subzones which, given sufficient shelter from wave-action, become superimposed upon the Balanoid zone and interfere with the barnacles. They are local in two senses: (a) they occur on British rocky coasts only under certain conditions; and (b) they occur only over a certain region of the northern hemisphere, and are not even universal in Europe. Another example of a special zone is the *Patella cochlear* belt of South Africa. This again occurs, in South Africa, only under certain conditions; and, although covering more than a thousand miles of coast, is limited to South Africa. From the account given by Cranwell & Moore (1938) of the Poor Knights Islands, New Zealand, it seems probable that there again additional zones must be recognized. But all these special zones are in one sense or another *local*, whereas the three basic zones approach much more nearly to universality. Furthermore, in view of the enormous numbers of variations in tidal range and behaviour, and in degrees of wave-action which occur in the world, it cannot be expected that everywhere the existence of the three primary zones will be realized in a simple form so that they are superficially obvious to the eye on a first inspection of the shore. They may be obvious, as on some of the western coasts of Scotland; but elsewhere the zonation may at first sight seem to have little relation to them, and it is only on detailed study that their reality appears.

(5) *The local absence of ecologically important species.* This is a line of inquiry to which we should like to direct the attention of future workers, as it may in time lead to very interesting discoveries. It has a bearing on the zonation problem, as some at least of the species concerned are forms which commonly characterize zones. Before our recent visits to America we had supposed—and this supposition is certainly widely held among marine biologists—that on any rocky coast subject to average environmental conditions there would be a fairly standard set of plant and animal forms represented. In other words, if any locality were free from restricting influences such, for instance, as those which prevail in an estuary, one would expect to find on the shore species of periwinkles, acorn barnacles, crabs, limpets, anemones, whelks and other common forms of life. There are certain 'ecological niches' such as those tenanted on many shores by limpets, which one might always expect to find occupied by these animals, although it is well known that in different parts of the world they are filled by different species. These may belong to different genera or different groups, but are still 'limpets'. Thus many limpets are Prosobranchs, while others (*Siphonaria*, *Gadinia*) are Pulmonates; *Patella* is a leading genus in some parts of the world, *Acmaea* in others; but it is so general a feature of shores that limpets of some kind are common on open rock surfaces that it is difficult to believe that on some shores

there are none. Yet this seems to be the truth. On the south-east coast of the United States, for instance, the common limpets of Florida are Siphonarias; but during our stay in North and South Carolina we could not find a single open-rock limpet of any sort. There are under-stone limpets (*Crepidula*, *Diodora*) there, but these belong to quite a different ecological sphere, the cryptofauna. Farther north again, *Acmaea testudinalis* becomes plentiful on open rock, but even within its range there are shores which lack it, and in any case it appears to be a less dominant limpet than the British and South African Patellas. We also found examples in other groups—there seem to be rocky shores lacking (or almost lacking) periwinkles, whelks, crabs, anemones and barnacles. In some cases the absence can be explained as, for instance, a reduction of barnacles in marine inlets separated by intricate channels from the open sea, or an absence of limpets on rocks which are scraped by ice during the winter. Some of the absences again may be seasonal. But when these explanations have been applied, there remain examples which at present seem inexplicable. We do not consider that the cases of absence which we have ourselves observed are as yet fully established, because it is not an easy matter to certify the complete absence of some species from a locality, especially during a short time. A fuller search over a longer period is needed. At the same time the apparent absences we have noted are certainly not to be put down to defective observation. After working on the shore over 25 years two experienced people cannot spend several weeks working in a district, keeping a watch for limpets all the time (and having found thousands the month before a few hundred miles away), and see not a single one, unless limpets, at that place and season, are at least very scarce. While, therefore, we feel that confirmation is needed, we shall be much surprised if the general position here outlined does not prove to be correct.

TERMINOLOGY

On the assumption that the three basic zones are more or less world-wide in distribution, it would be desirable to find names for them which do not depend on the occurrence in each of some particular organism. This has been achieved in the case of the sublittoral fringe, a term introduced by us in 1937 (pp. 352, 360), which has worked well in practice. The names Littorina and Balanoid zone are satisfactory in the main, as the belts to which they refer do, on all the more typical shores, support a population of Littorinae and acorn-barnacles respectively; but it is quite possible to find shores on which, in the Balanoid zone, barnacles are few or even absent, and also shores with few if any Littorinae. In the absence of these animals, however, the zones themselves can still be recognized, they are real entities. We have discussed a possible improved terminology with many marine biologists, and have gradually worked out the system introduced below. Dr Wesley Coe of the Scripps Institution would like it to be simply 'upper, middle and lower' zones. As we are ourselves much in favour of simplicity, we are not averse to this, but it has practical disadvantages. For instance, the Balanoid zone is commonly divided into upper and lower subzones, and while it is satisfactory to refer to the 'upper Balanoid zone' it is less suitable to speak of the 'upper middle zone'. Also, the terms proposed are not in the least descriptive, and bring nothing particular to one's mind. After long consideration we propose the name *supralittoral fringe* as an alternative to 'Littorina zone'. This is descriptive and accurate; and just as the sublittoral fringe is the fringe or boundary zone between the tidal and subtidal areas, so is the Littorina zone the upper fringe of the tidal area, the boundary

belt between land and sea. The only objection to *supralittoral* which we have encountered lies in the fact that on a printed page it looks very like *sublittoral*, and in reading over our own notes we find that the eye often confuses the two, with unfortunate results. This is quite a serious drawback, and we therefore propose to substitute the word *infralittoral* for *sublittoral*; it means much the same thing and does not visually resemble *supralittoral*. The most difficult zone to re-name is the Balanoid. This is the middle zone on the shore, the most fully intertidal, and in view of the fact that at least part of it tends to uncover twice a day, could be referred to as the 'semidiurnal zone'. This would not, however, cover it for regions where the tides are *not* semidiurnal, and on the whole we favour the name *midlittoral zone* as being in keeping with the other terms proposed. We therefore formally propose that the three main zones of the shore be called:

Supralittoral Fringe

Midlittoral Zone

Infralittoral Fringe

and that these terms be applied in the same sense as the terms 'Littorina zone', 'Balanoid zone' and 'Sublittoral fringe', used on p. 292. The belts thus named are represented graphically in Fig. 3.

How far is this system in keeping with the terminologies introduced locally by previous workers? Needless to say there has been no general agreement and no general practice, otherwise it would not be necessary to introduce a new scheme. It would probably be true to say that many workers have recognized the reality of the three zones, but their reactions to them have been very various. The term *supralittoral* has often been used, though not always as a synonym for our Littorina zone. Some authors have substituted *subterrestrial*, but this sounds too much like *subterranean* and has therefore no advantage over *supralittoral*. The word *midlittoral* is less common, though it has been used by Dakin *et al.* (1948) in their recent account of the New South Wales coast, even if not as an exact equivalent of our Balanoid zone. The word *sublittoral* is common enough in the literature, though as usual it is used in several senses; but Feldmann (1938) introduced the term *infralittoral* as being more analogous with *supralittoral*, and for the reasons given above we prefer this. Dakin *et al.* (1948) have introduced another term, 'littoral-sublittoral fringe', but this is not only cumbersome but unnecessary, as it is the same thing as our sublittoral (=infralittoral) fringe. Moreover, it directly uses the word *littoral* itself (as distinct from its combinations), and that introduces difficulties to which reference will be made below. From all this it will be seen that the system we propose does not depart very fundamentally from previous usage, but it seeks to standardize this and to choose those words which will be most generally suitable and most widely applicable. We would, however, draw attention to our use of the word *fringe*, in connexion with the adjectives *supralittoral* and *infralittoral*. This is our personal contribution, and it has the advantage of indicating that both the zones designated are boundary-belts, literally the upper and lower fringes of the tidal area; and it avoids linking them up too closely with any specific tidal levels with which, as will be explained below, they do not necessarily coincide.

There is one fence left to climb. If we use combinations such as *supra-* and *infralittoral*, what is their relation to the word 'littoral' itself? We have avoided using the latter word as far as possible in our own papers, because it is given such widely different meanings by different authors: hence our use of the terms *intertidal zone* or *tidal belt* for the whole region between extreme high and low water of spring tides. The term 'littoral zone' has

three main usages in the literature: (i) as the equivalent of our intertidal zone; (ii) as the equivalent of our midlittoral zone (i.e. something narrower than the whole intertidal zone); and (iii) as covering not only the intertidal zone (and sometimes including higher levels)

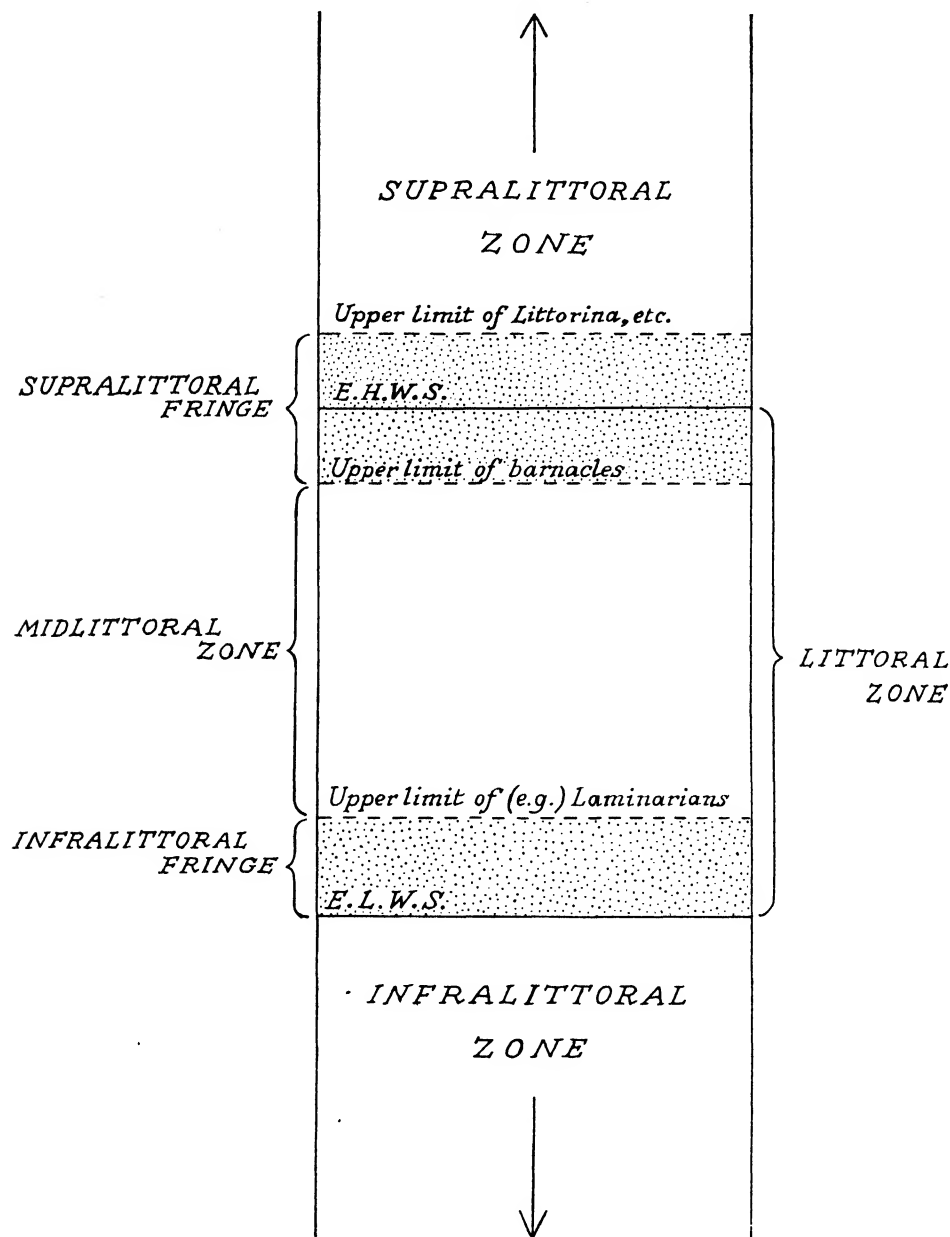


Fig. 3. Diagram illustrating the terminology introduced in the text; see pp. 297-302.

but also the whole submerged surface of the continental shelf. If we ourselves have to choose between these meanings we would prefer to make littoral the equivalent of intertidal (probably the classic usage), as this makes the term 'infralittoral zone' available for

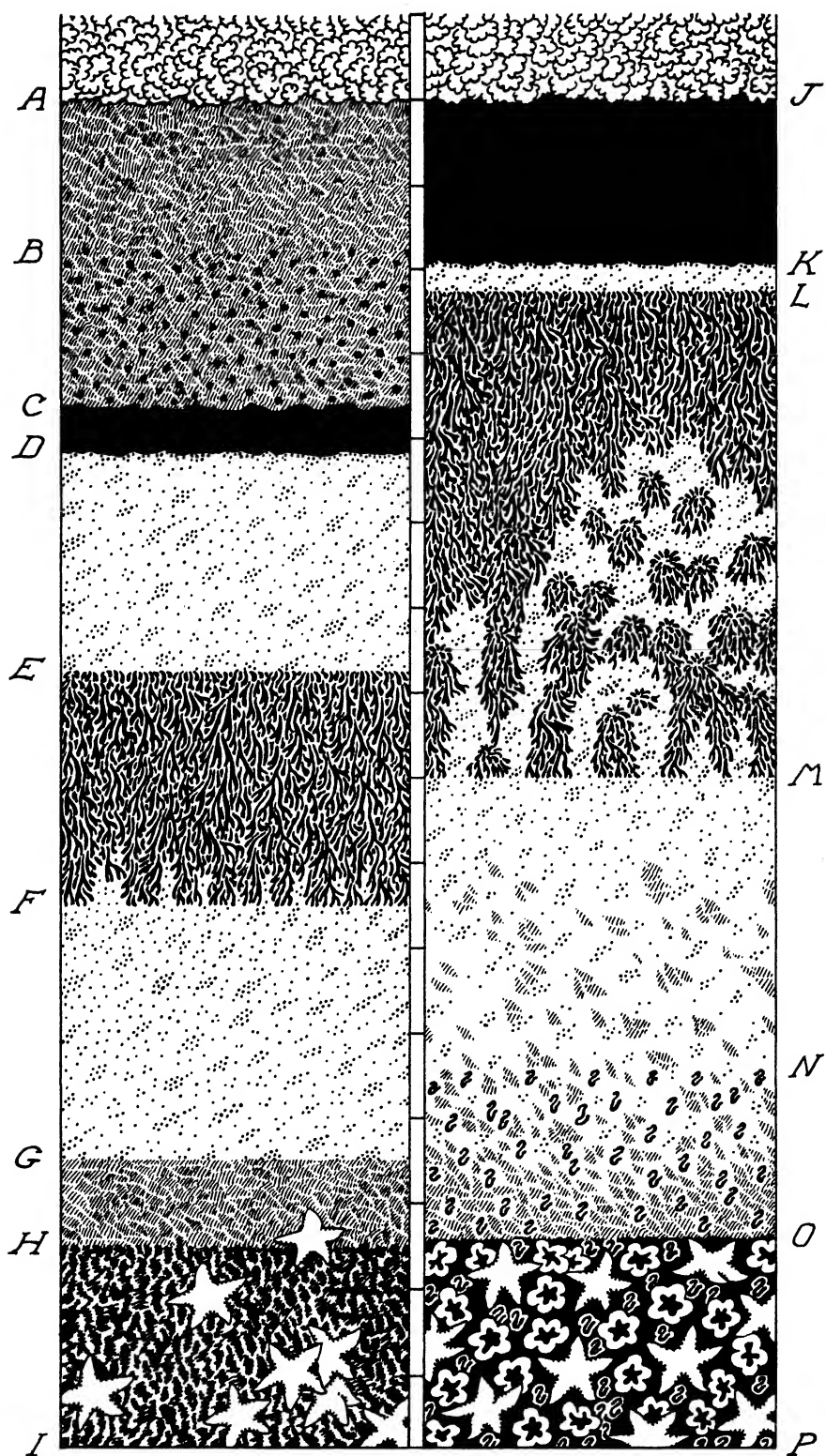


Fig. 4.

the zone extending from extreme low water to the edge of the continental shelf (with our infralittoral fringe as its upper border), and the term 'supralittoral zone' available for the maritime region above high water, of which our supralittoral fringe includes the marginal part.

Lastly we cannot altogether pass over the terminology to be applied to plant and animal communities within the several primary zones of the shore. It is well known that, although a single zone or subzone may be occupied throughout a long stretch of coast by one and the same community, in many cases a given zone will be occupied by a complex patchwork of different communities. So many of these patches and subzones are of local occurrence that it is difficult to see how any universal terminology can be devised for them, and it seems to us unobjectionable to speak of a 'Pyura subzone' or a 'Pyura community' as occurring in the broader zone known as the infralittoral fringe. This usage has been employed very intelligibly by a number of authors as, for instance, by Feldmann in his excellent account of the algae of the western Mediterranean. But we are very doubtful whether it

Fig. 4. A diagram illustrating the impossibility of attempting to define zones in terms of tidal levels, in view of the marked differences in level of some of the zones and zone-boundaries on the two sides of a small island. The first column shows the zonation on the sloping, sunny, southward-facing slope of Brandon Island (in Departure Bay, British Columbia); the second column the zonation on the shady, cliffed, northward-facing side (see also Pl. 8). The two sides are less than 100 yards apart, are subject to similar degrees of (relatively slight) wave-action and are differentiated only by the features already mentioned. It will be noted that the *Fucus* zone (*EF*, *LM*), the upper limit of the majority of barnacles (*D*, *K*) and the black zone (*CD*, *JK*) are at quite different levels on the two sides. The details are as follows:

- A* Lower limit of macroscopic maritime land-lichens.
- B* Upper limit of the majority of Littorinae.
- C* Upper limit of the densest blackening (due here at least partly to impoverished *Hildenbrandia*).
- D* Upper limit of main barnacles.
- E* Upper limit of main growth of *Fucus*.
- F* Lower limit of main growth of *Fucus* (chiefly *F. furcatus*).
- G* Lower limit of main barnacles.
- H* Upper limit of infralittoral fringe, which is here dominated by a dense brown beard-like growth consisting of diatoms and small Rhodophyceae, and by very large violet starfish (*Pisaster ochraceus*).
- I* Level of extreme lower low water of spring tides in July 1947.
- J* Lower limit of macroscopic maritime land-lichens. This is also approximately the upper limit of *Littorina* and the level of extreme higher high water of spring tides in July 1947.
- K* Upper limit of main barnacles.
- L* Upper limit of main *Fucus*.
- M* Lower limit of main *Fucus*.
- N* Approximate upper limit of most *Serpula*.
- O* Upper limit of infralittoral fringe, dominated on these shaded slopes by a community of violet starfish (*Pisaster ochraceus*) with anemones (*Metridium*) and *Serpula*.
- P* Level of extreme lower low water of spring tides in July 1947.
- AD*, *JK* Supralittoral fringe. In the first column this has only a slight blackening, maximal in its lower part (*CD*); in the second, it is blackened throughout by *Verrucaria striatula* and other forms, and also inhabited by *Littorina*.
- DH*, *KO* Midlittoral zone. In the first column this is occupied almost throughout by barnacles, although it has a belt of *Fucus* (hiding the barnacles) in the middle, and a narrow bare zone (*GH*) at the bottom, where the barnacles are reduced. In the second column the *Fucus* belt is higher up, the barnacles fade away gradually below, and the lower part of the zone is invaded by *Serpula*.
- HI*, *OP* Infralittoral fringe.

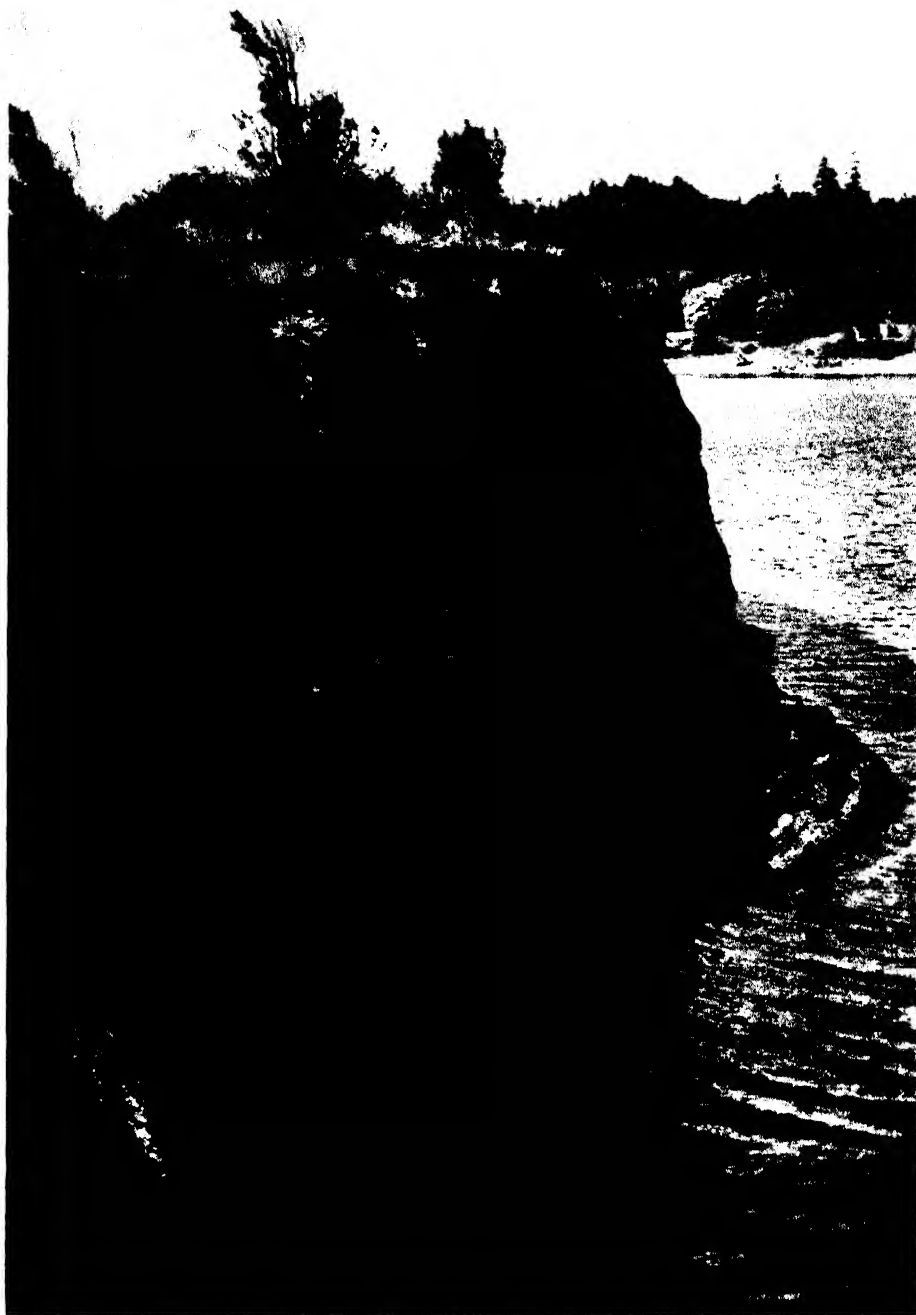
(The scale is shown in feet between the two columns. The figure deals only with the distribution of the main populations of selected species—outlying patches of barnacles, *Fucus*, etc., follow different rules from the main populations, and will be dealt with in detail elsewhere.)

is usefully possible to go much further than this, at any rate unless it can be done along new lines rather than along any as yet laid down. There is a school of ecologists who seem to feel that it is more scientific to say 'The undersigned executed autotrophic reactions in relation to the Graminetum' than to say 'We had tea on the lawn'. This is doubtless a delusion; but it has led to a positively terrifying outburst of terminology referring to communities. We have read many papers which use these terms: but we can never convince ourselves either that they have substantial advantages or that they do much to advance our knowledge. For our own part, therefore, we propose to continue to refer to a mussel-bed as a mussel-bed, and not as either a 'Mytiletum' or as 'an example of the *Mytilus-Balanus* Biome without the *Balanus*'. One cannot help recalling Charles Singer's characterization of this ecological terminology, in his book *A Short History of Biology* (1931, p. 279), where he says: 'From the beginning, however, it [ecology] has been cursed, more than most sciences, by a horde of technical terms equally hideous, unnecessary and obfuscating.'

RELATION OF ZONES TO TIDAL LEVELS

In the short definitions of the three zones given above (p. 292) they are related only very approximately to tidal levels. This is intentional because, although we believe the zones themselves to be persistently recurrent, their relation to tide-levels is not necessarily a matter of exact coincidence, and varies according to the nature of the shore. One cannot, having determined a given level (e.g. mean low water of neaps), expect to find that this coincides exactly with a boundary between two zones. Sometimes it does; but in other cases the boundary is *related* to a tidal level rather than coincident with it. Moreover, the relation between zones and levels may be different, on the same shore, at points only a few yards apart (Fig. 4). The levels of high and low water vary progressively from day to day, and while it is not yet clear whether we must attach most importance to mean levels or extreme ones (more likely both are effective), it is clear that the relation of levels to zones is complex. The zones are therefore best defined in terms of organisms. In the usage here advocated, the upper limit of the infralittoral fringe is that of the bulk of the population, on open rock, of some dominant organism (e.g. *Laminaria*, *Pyura*) which inhabits it: this is also the lower limit of the midlittoral zone. The upper limit of the midlittoral zone (= lower limit of supralittoral fringe) is the upper limit of barnacles in quantity (or of some equivalent organism if the barnacles are missing). The upper limit of the supralittoral fringe may be fixed as is locally convenient—e.g. by the upper limit of *Littorina* or the lower limit of maritime land-lichens. This usage fixes the boundaries by means of the organisms; and the tidal levels are then found to be related to them in a definite way even though not necessarily coincident with them.

Zones between tide-marks have no constant *depths* whatever. Tidal behaviour and tidal ranges vary so much in different parts of the world that no such constancy is to be expected; and the depths of zones are controlled not only by tidal phenomena, but also by variations in amount of wave-action, distribution of sun and shade, and other features. This means that even on a single stretch of coast with the same tidal range, the zones may vary in depth from one rocky face to another. It is possible that if enough measurements were made, and if a sufficient number of corrections were applied to them (for differences in tidal range, exposure to wave-action, sunshine, etc.), a constant *proportion* between the depths of the main zones could be demonstrated; but this has not been ascertained. The *widths* of zones naturally vary in relation to the slope of the rock, apart from the factors



Part of the cliffed, shaded northern coast of Brandon Island, in Departure Bay, British Columbia. This supplements Fig. 4, and shows, as a continuous grey band, the very marked black zone of *Verrucaria striatula*, etc., and below this the very sharp white line representing the upper limit of the majority of the barnacles. Below this barnacle-line are dark patches of *Fucus* overgrowing the barnacles and with their upper limit only a few inches below that of the barnacles. Above the *Verrucaria* zone the pale lower limit of the larger maritime land-lichens can also be seen. (Photograph by Anne Stephenson.)

which control their vertical depth. Thus a zone which, on a vertical wall, is a foot deep, may also occur on a nearly horizontal rocky platform where, although its vertical extent may still be only a foot, its width may be many yards.

A mistaken idea, which is commonly held, is that intertidal zonation is a result of tidal action. This is not so. Zonation occurs, both above and below the water-level, round static waters such as ponds and lakes, where there is no tidal change.* The primary cause of it is the existence of an interface between air and water. Below the surface of the water there is a gradient in light-penetration, and this can be accompanied by other gradients such, for instance, as a change in sedimentation with increasing depth. Zonation results from these gradients. Above the water-surface there is further zonation, controlled by the degrees to which the surrounding rock-surfaces are exposed to influences emanating from the body of water or connected with its presence—such as spray, or moisture formed during evaporation. In a marine area with no tide and no wave-action there would thus be zones corresponding to our supralittoral and infralittoral zones at once, each with its subzones. If we add considerable and steady wave-action but no tide, we produce a third zone, the littoral, related to the average amplitude of the waves. We therefore have all the essentials of intertidal zonation without any tide at all; but naturally if tidal action is added to the effects of wave-action and of an interface between air and water, the zonation is strengthened and made more marked. We cannot, however, make any general statement to the effect that zonation is more marked where the tidal range is great than where it is small, because it is now well known that very marked zonations can occur with small tidal ranges; and the zonation in the Bay of Fundy, where the tidal range is maximal, is no more elaborate than anywhere else, in fact it is less marked (in the places we have visited) than on the Atlantic coast of Nova Scotia where the range is much less. It is also a feature of zonation which has struck a number of observers that the zones are often very sharply marked in places where the oceanic surge is so constant that much of the rock is wet in almost any weather and at almost any state of the tide, so that the existence of sharp zonal boundaries becomes peculiarly difficult to explain. That the argument of this paragraph is not fanciful is well illustrated by the state of affairs in the Mediterranean. While that sea is not, as generally imagined, literally tideless, there are many parts of it where the tidal amplitude is small (e.g. rarely exceeding a foot), and where the sea-level varies a good deal more in accordance with irregular changes in barometric pressure and in force and direction of wind, than it does as a result of tidal action. (This is illustrated graphically by, for instance, Feldmann, 1938, p. 31). As Feldmann has shown, for the stretch of the Mediterranean coast of France nearest to Spain, the three usual zones exist, but the midlittoral is apparently very narrow in sheltered places, achieving a much more distinct existence where there is considerable wave-action.

SUMMARY

On the basis of 30 years' first-hand experience of rocky coasts in Britain, North America, South Africa, the Indian Ocean and Australia, it is suggested that certain features of zonation between tide-marks are of such widespread occurrence in the world that they may even be universal. The terminology applicable to the widespread zones is discussed, and a scheme is proposed which defines them and attempts to name them appropriately.

* It is true that the water-level in ponds and lakes can change owing to rain or evaporation, and that this variation can affect the zonation; but this is an irregular variation unlike that of the tides and hardly affects the present argument.

The zonation of open rock-surfaces exposed to degrees of wave-action intermediate between maximal and minimal is regarded as the standard from which deviations may most conveniently be recognized. From above downwards shores tend to show the following belts:

(1) *Supralittoral zone*. The maritime belt lying near the sea, above tide-marks, but subject to some maritime influence (e.g. to finely divided spray in rough weather). The lower limit of this zone is the same as the upper limit of the one below. Its upper limit is not within the scope of this paper.

(2) *Supralittoral fringe*. From the upper limit of barnacles (in quantity) to the nearest convenient landmark above this (e.g. the upper limit of Littorinae or the lower limit of maritime land-lichens or flowering plants). High water of spring tides invades at least the lower part of this zone.

(3) *Midlittoral zone*. From the upper limit of barnacles (in quantity) down to the upper limit of the zone below. This belt tends to be covered and uncovered every day, at least in part.

(4) *Infralittoral fringe*. From the upper limit of any convenient dominant organism (e.g. *Laminaria*, *Pyura*) to extreme low-water level of spring tides, or to the lowest level ever visible between waves. This zone uncovers only at the major tides, and sometimes only in calm weather.

(5) *Infralittoral zone*. From extreme low water of springs to a depth which has yet to be settled—it may be to the edge of the continental shelf or to the lower limit of seaweed vegetation.

An account is given of (a) the standard populations of these zones (p. 292); (b) of some of the principal variations in these populations (p. 293); (c) of the existence of additional local zones (p. 296); and (d) of the local absence of ecologically important species (p. 296). The terms littoral, supralittoral and infralittoral are discussed, in relation to others, and 'littoral' is defined as the equivalent of 'intertidal'. It is maintained that within the framework of the principal zones, subzones and patch-forming communities, which are much more local in occurrence, can suitably be named, as heretofore, from the organisms which dominate them. The relationship between the zones and tide-levels is discussed (p. 302), especially to emphasize that the zones cannot be defined in terms of tidal levels although related to these, but must be defined in terms of the distribution of organisms.

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THE VEGETATION OF THE NORTH-WESTERN CONWAY VALLEY, NORTH WALES

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(With two Figures in the Text)

INTRODUCTION

The north-western Conway valley was chosen for these studies, because documentary evidence of the process of human settlement, and the nature of land utilization from the early fifteenth century for the area was available in the Baron Hill MS. (housed at the University College, Bangor).

By collating historical and ecological studies, it might be possible to determine the role of specific aspects of human interference, in the development of certain plant communities. The data presented in these studies were collected primarily during the summers of 1939 and 1940, supplemented by further observations made since 1945.

The district studied extends from the River Porthllwyd in the south, to the estuary of the Conway in the north. Its eastern boundary is formed by the Conway, and its western by the northern section of the Carnedd ridge (comprising Y Foel Fras, 942 m. (3090 ft.); Y Gledr Ffordd, 762 m. (2500 ft.); Drum, 771 m. (2528 ft.); Drosogl, 619 m. (2030 ft.); Talyfan, 610 m. (2000 ft.); Cefn Maen Amor, 412 m. (1350 ft.); and Mynydd Conwy, 246 m. (804 ft.)).

It is hoped to present these studies in four parts:

- Part I. Environmental factors (climatic and edaphic).
- Part II. Environmental factors (human interference).
- Part III. Woodlands and related vegetation.
- Part IV. Upland vegetation.

I wish to acknowledge the encouragement, and valuable advice given by Prof. R. Alun Roberts, in whose department this work has been carried out. Similarly, to Prof. G. W. Robinson who has allowed me to use the soil data referred to in Part I of these studies, and for his valuable advice in matters concerning the soil.

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PART I. ENVIRONMENTAL FACTORS (CLIMATIC AND EDAPHIC)

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I. CLIMATIC FACTORS

Not all the climatic data of importance in ecological studies are available for the area, thus use must be made of data drawn from stations on its immediate periphery.

(1) RAINFALL

(A) *Lowlands*

From Table 1 there is seen a gradient of rainfall from the coastal low rainfall area at Conway (860 mm. (33·84 in.)), and Llandudno (763 mm. (30·04 in.)) to the more inland southerly higher rainfall area at Rowen (1284 mm. (49·42 in.)), and Trefriw (1378 mm. (54·23 in.)). The rainfall in the northern area is distinctly lower than in the more westerly Welsh coast, e.g. Abersoch (1146 mm. (45·12 in.)), and Aber (998 mm. (39·3 in.)), while the southern area also has a lower rainfall than in some western valleys, e.g. Beddgelert (2364 mm. (93·06 in.)). These features can be accounted for by the lee position of the Conway Valley in relation to the prevailing south-westerly winds.

Table 1. *Mean annual rainfall of Snowdonian and Conway Valley stations*

	Altitude (m.)	Mean annual rainfall (mm.)
A. Lowland stations		
(a) Western stations:		
Abersoch*	31 (100 ft.)	1146 (45.12 in.)
Beddgelert*	41 (133 ft.)	2364 (93.06 in.)
Aber†	15 (50 ft.)	998 (39.3 in.)
(b) Conway Valley stations:		
Conway (Castle Bank)‡	15 (50 ft.)	860 (33.84 in.)
Llandudno§	22 (71 ft.)	763 (30.04 in.)
Rowen‡	43 (140 ft.)	1255 (49.42 in.)
Trefriw Wells‡	8 (25 ft.)	1378 (54.23 in.)
B. Upland stations		
(a) Main Snowdon massif:		
Snowdon (Gauge No. 14)*	96 (315 ft.)	3018 (118.81 in.)
Snowdon (Pen-y-Gwryd)*	278 (913 ft.)	3432 (135.14 in.)
Snowdon (Gauge No. 8)*	714 (2340 ft.)	4576 (180.14 in.)
Llyn Ogwen*	306 (1004 ft.)	3077 (121.15 in.)
(b) Conway Valley:		
Llyn Cowlyd	493 (1617 ft.)	2119 (83.42 in.)
Llyn Eigiau	379 (1245 ft.)	1978 (77.88 in.)
Llyn Dulyn	498 (1632 ft.)	2020 (79.32 in.)
Llanbedr-y-Cennin‡	155 (509 ft.)	1540 (60.63 in.)
Penmaenmawr‡	366 (1200 ft.)	1294 (50.95 in.)
(mountain reservoir)		

* Carr & Lister, *The Mountains of Snowdonia*, 1925. Appendix 5. Table 5 compiled by A. Lockwood.

† College Farm, Aber, for period 1933–43.

‡ 1918–29 inclusive from *British Rainfall*.

§ *Book of Normals*, H.M.S.O. (for period 1881–1915).

|| Data compiled by the North Wales Power Co. Ltd., for period 1924–45 inclusive.

(B) Uplands

The lee position is reflected again in the lower rainfall at equivalent altitudes of the Conway Valley uplands, when compared with the main Snowdonian massif. From Table 1, there is an increase of rainfall from the northern low rainfall area (extending from Conway Mountain to the north slopes of Talyfan (1016–1270 mm. (40–50 in.)), to a southern high rainfall area (1651–2032 mm. (65–80 in.)) in the Porthllwyd-Dulyn lateral valleys). Robinson & Wasowicz (1935) conclude that rainfall is in excess of 2500 mm. (100 in.) per annum at high altitudes in the vicinity of Foel Fras.

(C) Seasonal distribution

No data are available for the Conway Valley, thus values for proximate stations (Aber and Llandudno) are set out in Table 2.

Table 2. *Seasonal distribution of rainfall in millimetres (Aber and Llandudno)*

Month	Aber*	Llandudno†
January	122 (4.79 in.)	66 (2.58 in.)
February	85 (3.33 in.)	53 (2.08 in.)
March	72 (2.82 in.)	55 (2.17 in.)
April	52 (2.03 in.)	46 (1.81 in.)
May	62 (2.45 in.)	48 (1.90 in.)
June	59 (2.32 in.)	52 (2.03 in.)
July	71 (2.80 in.)	61 (2.39 in.)
August	59 (2.33 in.)	77 (3.02 in.)
September	77 (3.02 in.)	58 (2.28 in.)
October	135 (5.30 in.)	91 (3.59 in.)
November	99 (3.91 in.)	78 (3.09 in.)
December	107 (4.20 in.)	79 (3.10 in.)
Mean annual rainfall	998 (39.3 in.)	763 (30.04 in.)

* College Farm, Aber, for period 1933–43.

† *Book of Normals*, for period 1881–1915.

One can only surmise that the seasonal distribution of rainfall in the lowlands of the Conway Valley, is similar to that of Aber at the southern, and to Llandudno at the northern, end of the district. Both stations are distinctly oceanic, in that they have high autumn and winter, and lower spring and summer values. October is the wettest month, but much higher values are seen at Aber than at Llandudno. April is the driest month at both stations.

(2) TEMPERATURE

As no data are available for the district, those for Bettws y Coed and Llandudno are given in Table 3.

Table 3. *Maximum, minimum, and mean monthly temperatures (Bettws-y-Coed and Llandudno)*

Month	Bettws-y-Coed*			Llandudno*		
	° C.			° C.		
	Max.	Min.	Mean	Max.	Min.	Mean
January	7.2	1.4	4.4	7.4	2.9	5.2
February	7.7	1.4	4.6	7.8	2.9	5.3
March	9.0	1.9	5.4	8.8	3.3	6.1
April	11.8	3.6	7.7	11.4	5.0	8.2
May	14.9	6.1	10.6	14.4	7.6	11.0
June	18.0	9.1	13.6	17.5	10.6	14.1
July	19.1	10.6	14.9	18.9	12.3	15.6
August	18.7	10.6	14.6	18.6	12.3	15.5
September	17.1	8.2	12.7	16.9	10.8	13.9
October	12.9	5.5	9.2	13.2	7.9	10.6
November	9.5	3.2	6.4	10.3	5.4	7.8
December	7.8	2.2	5.0	8.3	3.7	6.0
Mean annual temp.	12.8	7.3	9.9	12.8	7.1	9.9

* *Book of Normals*, for period 1881–1915.

The greater oceanicity of Llandudno is emphasized by its warmer winters and summers, compared to Bettws-y-Coed. As the stations are at the extreme northern and southern limits of the Conway Valley, respectively, the district studied (within its lowlands) can be considered to have temperature conditions intermediate between them.

Temperatures range between 1° C. (34° F.) in January, and 15° C. (59° F.) in July, at higher altitudes in the district. Snow cover in winter is intermittent, locally it may remain into the spring months. The ground is only occasionally frozen in winter (Robinson & Wasowicz, 1935).

(3) SUNSHINE

Sunshine data are summarized for Aber and Llandudno in Table 4.

Table 4. *Mean daily hours of sunshine (Aber and Llandudno)*

	Aber*	Llandudno†
January	2.15	2.48
February		1.84
March		4.00
April	6.31	5.77
May		6.94
June		7.20
July	4.61	6.39
August		5.77
September		4.93
October	1.57	3.35
November		2.07
December		1.29
Mean per month	3.66	4.34

* College Farm, for period 1940–5.

† Data from the *Book of Normals* for period 1881–1915.

'Key' to place names in Fig. 1

- | | | |
|---------------------------------------|------------------------|------------------------|
| 1. Conway | 20. Tyn-y-groes. | 39. Rowlyn Isaf. |
| 2. Coetmor Woods. | 21. Rowen. | 40. Rowlyn Uchaf. |
| 3. Penmaenmawr. | 22. Maen-y-bardd. | 41. Hafod-y-gors-wen. |
| 4. Llanfairfechan. | 23. Cae-côch. | 42. Ffridd-y-bont. |
| 5. Aber. | 24. Tan-y-braich. | 43. Cerrig Cochion. |
| 6. Gyffin. | 25. Hafoty Gwyn. | 44. Maen-eira. |
| 7. Benarth. | 26. White Hart. | 45. Hafod-y-garreg. |
| 8. Bryn Mawr. | 27. Gors-wen. | 46. Dolgarrog. |
| 9. Hendre. | 28. Dol-y-Castell. | 47. Bryn Gwenith. |
| 10. Groesffordd. | 29. Coed Bedw. | 48. Waen Bryn Gwenith. |
| 11. Llechan. | 30. Caerhun. | 49. Dolgarrog Woods. |
| 12. Hen-rhŷd. | 31. Conovium. | 50. Trosbwl. |
| 13. Reservoir (Penmaenmawr mountain). | 32. Bron-y-Gader. | 51. Hafod-y-rhiw. |
| 14. Groes Ynyd. | 33. Llanbedr-y-cennin. | 52. Trefriw Wells. |
| 15. Llangelynin Old Church. | 34. Coed Ochr Gaer. | 53. Trefriw. |
| 16. Merchlyn. | 35. Pen-y-Gaer. | 54. Craig Eigiau. |
| 17. Erianws. | 36. Bwlch-y-Gaer. | 55. Morfa Conwy. |
| 18. Parc-y-Glyn. | 37. Tal-y-Bont. | 56. Llandudno. |
| 19. Llwydfaen. | 38. 'Soglog. | |

'Key' to symbols in Fig. 2

SILURIAN ROCKS



Sediments (slates, shales and grits).

ORDOVICIAN ROCKS

(a) *Sediments*

Primarily slates and shales.



Calcareous grits.

(b) *Volcanic rocks*

Acidic (rhyolites from Elles, 1909).



'Felspathic volcanic rocks' of the 1852 Geological Survey map (primarily of rhyolitic nature).



Coetmor ashes (Elles 1909).

(c) *Igneous rocks*

Acidic.



Basic (dolerites).

(d) *Complex of Ordovician rocks*

Complex of acidic (rhyolites), basic (pumice tuffs and spilitic agglomerates), volcanic rocks, dolerites and Ordovician sediments.

RECENT DEPOSITS



Alluvium and peat.



Wind-blown and estuarine sand.

There is a marked contrast in the mean daily hours of sunshine for these two stations Llandudno being much sunnier. Thus it is probable that the sunshine values for the northern part of the district approach those of Llandudno, while the southern part will be akin to Aber.

II. EDAPHIC FACTORS

As a background for the study of the soils, topography, geology and glaciation of the district are summarized below from the accounts of Ramsay (1881), Harker (1889), Elles (1909), Greenly, Montag, Boswell, Double & Fearnside (1927), Fearnside & Wilcockson (1928) and Davies (1936).

(1) TOPOGRAPHY AND GEOLOGY

Ordovician strata characterize the major part of the district, while Silurian rocks occur marginal to the Conway river.

The uplands are part of the north-eastern section of the Carnedd massif. They are set upon a pediment, of average height 244–274 m. (800–900 ft.), the edge of which rises steeply from the Conway. Immediately beyond the pediment lies an undulating mature drift covered upland (381–427 m. (1250–1400 ft.)). This then rises more steeply to the elevated mature contoured Carnedd massif, which includes within the district the Foel Fras tract, and the outlying eminence of Talyfan. Radiating from this elevated region are subsidiary ridges of essentially similar topography; locally, sharper features occur in relation to the occurrence of volcanic rocks or grits. In the lowlands, the Silurian area is more elevated than the adjacent Ordovician strata. It is also less glaciated, and of sharper topography. The Silurian strata are composed of slates, shales and grits. A similar range of sedimentary rocks occurs within the Ordovician area, but igneous and volcanic rocks are generally prevalent. Thus acidic intrusive rocks occur in the Foel Fras tract, which are, however, more basic than the extrusive rhyolites (Harker, 1889, pp. 41–2). Basic intrusives (dolerites) are frequent through the uplands, e.g. at Craig Eigiau, Melynlyn, Dulyn, Talyfan, and subsidiary ridges such as Pen-y-Cestyll, Pen-y-Gader, and Pen-y-Gaer.

From the early work of Ramsay (1881), extrusive volcanic rocks (contemporaneous, felspathic, porphyries, and ashes) are frequent in the uplands and pediment slopes. Harker (1889, pp. 24–5 and 28) states that the porphyries, and some of the felspathic ashes are rhyolitic; the former probably correspond to the rhyolites, and the latter to the rhyolitic tufts of the district south of the Porthllwyd river mapped by Davies (1936). Some of the felspathic ashes are also undoubtedly equivalent to the chloritic, felspathic, and calcareous, spilitic agglomerates, and pumice tufts described by Davies. It is of ecological interest that such rocks possessing an abundance of calcite are frequent in Coed Dolgarrog, and bear a similarity to the bedded pyroclastic series of Snowdon (Williams, 1927), containing 10.25% CaO, and 46.8% SiO₂, the flora of which have been described by Farmer (1925) and Woodhead (1932).

At Bryn Mawr, south of Conway, Ordovician calcareous grits occur.

(2) GLACIATION

The district has been intensely glaciated, the drift extending to 458–610 m. (1500–2000 ft.). It has been described as a very stony boulder clay (Fearnside & Wilcockson, 1928), highly indurated, and composed of local geological materials. In the drift emanating

from the lateral valleys, volcanic rocks are particularly abundant. No evidence was obtained of the penetration of the valley by the Irish sea drift, as had been considered a possibility by Fearnside & Wilcockson (1928).

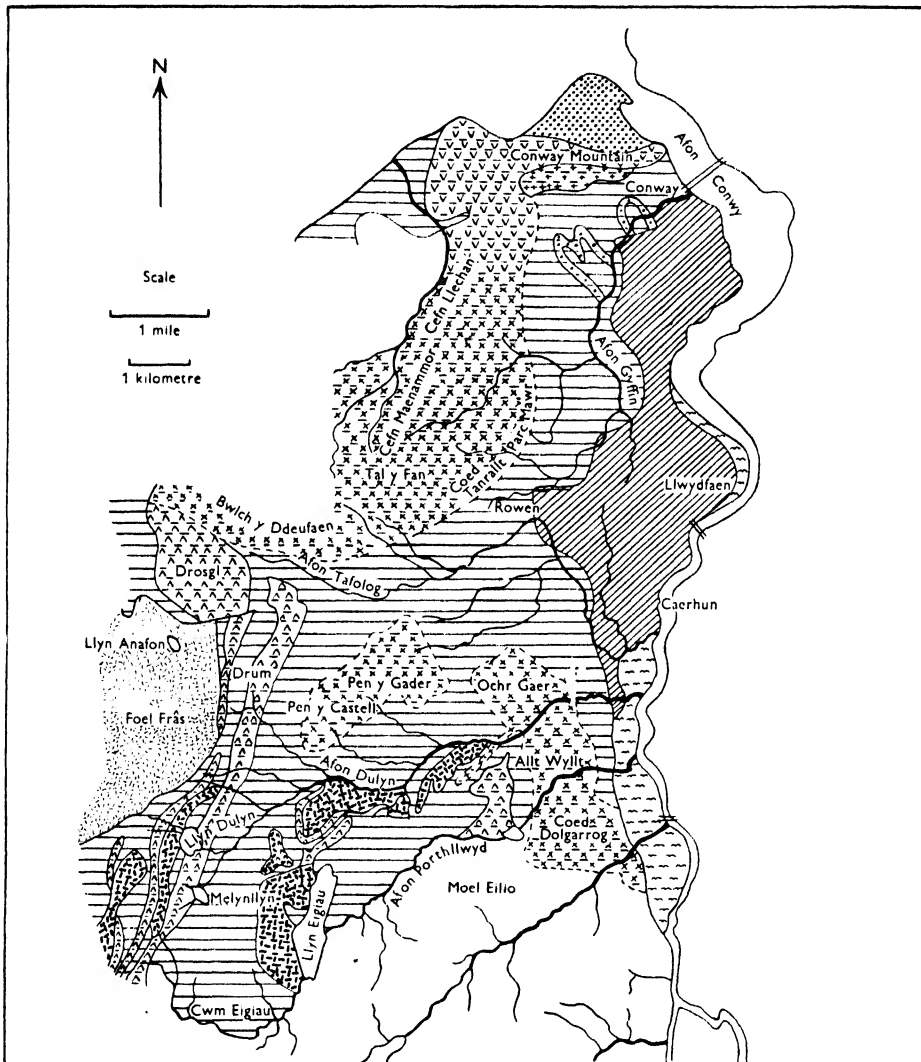


Fig. 2. Generalized geological map of the north-western Conway Valley. For 'key' see p. 311.

The drift of the main Conway Valley contains a greater proportion of sedimentary material; volcanic rocks are not abundant, and of these, rhyolites tend to be the most prevalent.

In the lowlands few areas are drift free, these being the elevated parts and steeper slopes of the Silurian area, and the calcareous grits near Conway.

(3) THE SOILS

The following terms are used in this account of the soils (following Robinson, 1936, p. 399):

Soil suite: a group of soils derived from the same, or similar, parent material. In pedological literature this is now termed the soil association. Here, however, the term suite, as suggested by Robinson (1936), is retained, to avoid possible confusion with the use of the association in plant ecological work.

Soil series: the soil suite is subdivided into a number of series, which are soils with similar profiles derived from similar parent material, under similar conditions of development.

According to Robinson (1934) brown earth loams of high organic matter content are the prevailing soil type, although, on account of the high rainfall of North Wales, it lies within the region of podsollic soils. This is accounted for by the resistance of loams to extreme eluviation, and the base reserves of the prevailing parent materials of the soils, i.e. igneous and sedimentary palaeozoic rocks. Podsoles would develop in relation to distinctly acidic parent materials, which are not prevalent.

The soils of the lowland of the north-west Conway Valley have been classified by Hughes & Walters (1935) as being within the Powys suite of soils, derived from the softer Ordovician and Silurian rocks. The uplands were not surveyed by them, but it can be stated that podsoles and their eroded derivatives become prevalent above 244–305 m. (800–1000 ft.). Extensive valley peats occur above 366 m. (1200 ft.), and blanket peats above 549 m. (1800 ft.). The latter have been studied by Robinson & Wasowicz (1935), and are classified as peat podsoles.

III. THE CLASSIFICATION AND DISTRIBUTION OF ENVIRONMENTAL FACTORS

The above is a general account of the environmental conditions within the north-western Conway Valley. A detailed account of their distribution will now be given, and an attempt made to classify environmental complexes as they occur in various parts of the district. The district is preliminarily subdivided into a number of areas, over which prevail a specific combination of environmental factors and related vegetational features. Altitudinal zones of vegetation delimit major areas of this nature. Each zone has its own particular tendency in soil development and general type of vegetation, these being climatically determined. The zones recognized are summarized in Table 5.

The zones are respectively subdivided into a number of subzones. A subzone is distinguished by: (a) its soils being members of the same suite; (b) specific climatic conditions prevailing over it; (c) a characteristic assemblage of plant communities.

Therefore the number of subzones occurring in a zone will depend on the range of soil parent materials present, and the variation within it in climatic conditions. The soil series of each subzone are classified in a manner similar to that of Glentworth (1944). The classification followed in this work is summarized in Table 6.

Many transitional types occur between closely related series, particularly in the case of the wetter soils. Where relevant, they are classified as such.

Over an area occupied by a soil series (i.e. the soil-series area) the environmental factors prevailing there can be summarized precisely in terms of the soil properties of the series itself, and the climatic factors prevailing over the subzone in which it occurs. Therefore, the soil series area, with its precisely definable environmental complex, is of first importance to the ecological study of plant communities.

The variation, intensity, and form of human interference in relation to various zones and subzones will be dealt with in a subsequent paper.

Table 5. *Altitudinal zonation of environmental factors*

Zone	Approx. altitudinal range (m.)	Approx. range of mean annual rainfall (mm.)	General tendencies in soil development	General vegetational features
I	0-152 (0-500 ft.)	889-1270 (35-50 in.)	Brown earths. Local tendency to podsolization (acidic parent materials)	Lowland oak woodland
II	610-2440 (200-800 ft.)	1016-1524 (40-60 in.)	Brown earths derived from basic, and podsoles from acidic parent materials	Transitional lowland-upland oak woodland
III	152-305 (500-1000 ft.) and locally 458 (1500 ft.)	1016-2032 (40-80 in.)	Range of soils similar to zone I, but soils of impeded drainage more prevalent	Upland oak woodland
IV	305-457 (1000-1500 ft.) and locally 549 (1800 ft.)	1016-2032 (40-80 in.)	Podsoles general, except in relation to basic parent materials	<i>Ulex gallii</i> acidic grasslands with heath
V	336-610 (1100-2000 ft.)	1905->2032 (75->80 in.)	Deep valley peat—gleys general	Bog vegetation, acidic grasslands, and heaths
VI	549-915 + (1800-3000 + ft.)	2032 (>80 in.)	Blanket peats (peat podsoles)	Blanket bog, and acidic grasslands

Table 6. *The classification of soil series*

Soil series	Conditions of development	Definition of resultant soil profiles	
<i>a</i>	Free drainage, with liability to seasonal drought	<i>a</i> ₁	Podsoles
		<i>a</i> ₂	Generally brown earths and some eroded podsoles of uplands
		<i>a</i> ₂ - <i>a</i> ₁	Soils of podsollic affinities with very acid surface humus, but leached <i>A</i> horizon absent
<i>b</i>	Equable moisture conditions, and very slight impeded drainage	<i>b</i>	Brown earths. In certain instances in the uplands they may be eroded podsoles now showing signs of slight drainage impedance, or eroded gley podsoles
<i>c</i>	Seasonally wet	<i>c</i> ₁	Gley soils with no marked surface organic material accumulation
		<i>c</i> ₂	Gleys with surface accumulation of organic material to a depth of 30 cm. (1 ft.)
		<i>c</i> ₃	Gley podsoles
<i>d</i>	Permanently wet	<i>d</i> ₁	Deep peat, depth of organic horizon at least 46 cm. (1 ft. 6 in.)
		<i>d</i> ₂	Deep peats, but superficial horizon dry
		<i>d</i> ₃	Peats shallower than 46 cm. (1 ft. 6 in.)
		<i>d</i> ₄	Gley soils with no marked surface accumulation of organic material

(1) THE ZONAL DISTRIBUTION OF ENVIRONMENTAL FACTORS

(A) *The environmental factors of zone I (lowland woodlands)*

The five subzones present have soils which are members of different suites. Well-developed podsoles are absent. There is a prevailing acidity and base deficiency in the soil, the degree of which depends on the base reserves of the parent material.

The major environmental factors of each subzone are summarized in Table 7.

A decreasing gradient of base reserves is evident in the parent materials of the soil, i.e. from subzone D → B → C and E → A. This is directly reflected in the degree of acidity

and lime deficiency of the derived soils. The relative prominence of individual soil series within the subzones is determined by topographical features and the perviousness of the parent material. Thus subzone A and subzone B, with pervious parent materials and sharp topography, have soils preponderantly free-draining. They contrast markedly with subzones B and C, whose soils have indurated and impervious parent materials, and have gently undulating glacial topography. Thus soils of equable moisture conditions, and to a lesser degree those of impeded drainage, are prevalent. The prevalence of soils of impeded drainage in subzone E is determined by the flatness and liability to flooding of the alluvial plain of the main Conway Valley.

Table 7. *The environmental factors of zone I*

Subzones ...	A	B	C	D	E
Range of mean annual rainfall (mm.)	889-1270 (35-50 in.)	889-1270 (35-50 in.)	889-1270 (35-50 in.)	889-1016 (35-40 in.)	889-1270 (35-50 in.)
Soil parent materials	Sedentary and colluvial Silurian sedimentary rocks	Glacial drift of lateral valleys	Glacial drift of main Conway Valley	Sedentary and colluvial calcareous grits	Alluvium of main Conway Valley
Tendencies in soil development	To podsolization	To brown earths	To brown earths	To brown earths	To series of impeded drainage
Topographical features	Sharp features frequent	Gently undulating	Gently undulating	Outcrops forming sharp features	Alluvial plain
Perviousness of parent material	Free drainage	Relatively impervious	Relatively impervious	Free drainage	?
Prevalence of soil* series					
a_1	—	—	—	—	—
a_2	4	3	2	5	—
a_2-a_1	2	—	—	—	—
b	2	4	4	—	2
c_1	2	3	2	—	4
c_2	—	1	2	—	—
c_3	—	—	—	—	—
d_1	1	2	2	—	2.5
d_2	—	—	—	—	—
d_3	—	2	—	—	—
d_4	1	2	1	—	—

* An arbitrary scale of 1-5 is used to denote relative prevalence of the soil series, thus: 5 = total occupation of subzone, to 1 = only occurring in very local patches.

(i) *Distribution of subzones*

Subzones A and B occupy the major part of the lowland zone, the latter probably the greater area. The Silurian region marginal to the Conway is occupied by subzone A primarily, while subzone B occupies the whole of the lowland Ordovician country, locally penetrating into the Silurian region, notably near Dol-y-Castell and Groes Ynyd. Subzone C occupies a relatively narrow band of country marginal to the Conway, primarily occurring over Silurian strata.

To the west of Conway lies subzone D, extending from near Gyffin to Bryn Mawr. The colluvial parent material of the soils frequently thickly overlies glacial drift near Conway. The alluvial flats of subzone E occur primarily below Dolgarrog, Tal-y-bont, and Llwydfaen.

(ii) *Summary of soil characteristics*

Generally, only soils of free drainage, and equable moisture conditions, have been studied in detail. Thus in the absence of excessive moisture, the effect of the parent material upon soil characteristics will be most clearly seen.

(a) *Soils of subzone IA.* Texturally, the soils of subzone IA are light loams. A typical soil development under conditions of free drainage is described in Table 8.

Table 8. *Soils of zone I, subzones A, B, C and D*

Horizons (cm.)	Description of soil	pH	Exchangeable CaO (%)	P ₂ O ₅ (%)	Exchangeable K ₂ O (%)
Subzone A					
(a) Benarth Woods, Conway, 46 m. (150 ft.) o.d. Drainage: free (parent material shale, and mud stone colluvium)					
0-15 (0-6 in.)	Loose fibrous organic layer, with much roots of <i>Luzula sylvatica</i>	4.18	0.21	0.0026	0.043
15-20 (6-8 in.)	Amorphous dark raw humus	3.93	0.08	0.0006	0.013
20-33 (8-13½ in.)	Dull, slightly yellowish duff-brown, loam soil	4.14	0.02	0.0001	0.011
33-51 (13½-20 in.)	Yellow brown loam	4.42	0.02	0.0001	0.011
51-67 (20-26½ in.)	Some angular stones with yellowish brown soil	4.48	0.02	0.0001	0.008
67+ (26½+ in.)	Angular stones (colluvium)	4.93	0.03	0.0001	0.006
(b) Parc-y-Glyn, Rowen, 46 m. (150 ft.) o.d. Drainage: free (parent material—fine-grained grits with mudstones)					
0-6 (0-2½ in.)	Amorphous raw dark humus	3.90	0.05	0.0008	0.009
6-20 (2½-8 in.)	Warm brown loam soil	4.00	0.02	0.0003	0.006
20-42 (8-16½ in.)	More rusty orange brown, loam soil	4.28	0.02	0.0003	0.005
42+ (16½+ in.)	Brownish grey soil, between dis-integrating grit	4.52	0.02	0.0003	0.009
Subzone B					
(a) Gorswen Wood, Rowen, 30 m. (100 ft.) o.d. Drainage: equable moisture conditions					
0-41 (0-16 in.)	Light greyish brown loam	4.55	0.05	0.0006	0.005
41+ (16+ in.)	Light grey, slightly iron mottled subsoil	4.79	0.07	0.0033	0.004
(b) As for (a)					
0-46 (0-18 in.)	Greyish brown medium loam	5.31	0.18	0.0014	0.007
46-76 (18-30 in.)	Light grey subsoil (slightly weathered glacial drift)	5.38	0.06	0.0020	0.012
76+ (30+ in.)	Greyish boulder clay, very compact and hard	5.21	0.07	0.0027	0.008
Subzone C					
Coed Bedw, Caerhun, 30 m. (100 ft.) o.d. Drainage: seasonally wet					
0-10 (0-4 in.)	Surface peaty horizon	4.10	—	—	—
10-25 (4-10 in.)	Brownish grey medium loam	3.96	—	—	—
25-62 (10-24 in.)	Brownish grey medium loam slightly iron mottled	—	—	—	—
62+ (24+ in.)	Grey compact boulder clay, many boulders	4.42	0.01	0.0007	0.012
Subzone D					
Wood at Hendre, Gyffin, 76 m. (250 ft.) o.d. Drainage: free					
0-15 (0-6 in.)	Dark brown loam soil	5.81	0.58	0.0001	0.041
15-46 (6-18 in.)	Dark brown loam soil	5.92	0.57	0.0008	0.004
46-84+ (18-33+ in.)	Dark brown loam soil	6.67	0.44	0.0006	0.003

The plant nutrient status of the soil is judged from the following standards:
CaO (exchangeable CaO %):

0.3 % and over	Satisfactory
0.2-0.3 %	Deficient
< 0.1 %	Very deficient

P_2O_5 (soluble in $N/2$ -acetic acid, shaken for 1 hr., ratio of soil to solution 1:40):

0.004 % and over	Satisfactory
0.002–0.004 %	Moderately deficient
0.001–0.002 %	Deficient
< 0.001 %	Very deficient

K_2O (exchangeable K_2O %):

0.012 % and over	Satisfactory
< 0.006 %	Deficient

Acidity was determined by the quinhydrone electrode method.

These standards represent the range of tolerance of agricultural crops to these individual soil factors. These standards clearly do not apply to individual native species, or plant communities, as their exact ranges of tolerance are not so precisely known. The use of these standards must be qualified in the light of this.

The soil profile features outlined in Table 8 are not those of a podsol. It can be described as a very acid, very lime, and phosphate-deficient brown earth, in which the surface organic layer has the properties of an acid A_0 horizon of a podsol. An alternative interpretation is that it is an eroded podsol, in the initial stage of the redevelopment of a podsol profile. From a study of the silica-sesquioxide ratios of similar soils in the uplands of North Wales, Robinson (1934) concludes that they are probably eroded podsoles. In the absence of silica-sesquioxide ratio data it is not possible to decide which of the foregoing interpretations is the correct one in the case of the profile discussed.

It is of interest that in the actual mineral soil, potash is not acutely deficient, but in the C horizon (67 cm. + (26½ in. +)) it is deficient. This suggests a partly organic origin for the richer potash content of the soil itself. Similarly, higher figures for lime in the surface organic horizon suggests its organic origin there.

The parent material in the above soil profile is composed of softer sedimentary materials. There are, however, no essential differences in acidity and plant nutrient status of soils derived from grits (Table 8).

Acidity in the soils of impeded drainage is not so marked, e.g. a peat had a pH of 5.01, and a permanently wet gley (5.09).

(b) *Soils of subzone IB.* Free-draining soils and those of equable moisture conditions are loams, as opposed to light loams in subzone IA.

There is neither visible evidence of podsolization, nor acid surface humus formation, as occurs in subzone IA, in the soil profiles examined (see Table 8).

The degree of acidity is appreciably less than in subzone IA (pH's ranging from 4.5 to 5.7 in soils of free drainage and equable moisture conditions). The exchangeable CaO status of the soils is poor, though the quantity present is approximately three times as great as that in the soils of subzone IA. Reserves of phosphate, though deficient, are approximately ten times those of the soils of subzone IA. As in the latter, potash is not markedly deficient.

The soil series with impeded drainage have a range of acidity similar to those which are free draining, the pH never falling below 5, and in one instance of a permanently wet peat soil reached pH 6.11.

The higher calcium status of subzone IB, when compared with IA, is attributed to the presence of basic volcanic rocks in the parent material. Similarly, the richer phosphate content appears to be a function of the parent material.

(c) *Soils of subzone IC.* Soils of this subzone have not been studied in as detailed a manner as those already dealt with. It is clear, however, that the soils are more acid in IC than in IB. Thus, the parent material is more calcium and phosphate deficient; this may be related to the very small proportion of basic volcanic rocks present in it (Table 8). Potash, however, is satisfactory. Soils of impeded drainage have a distinctly low range of pH, i.e. from 3.71 to 4.57. No evidence of extreme podsolization was seen in these soils in spite of the prevailing acidity. This may be attributed to their loam character.

(d) *Soils of subzone ID.* The soils derived from the calcareous grits are loams of a good crumb structure.

The soil described in Table 8 has a satisfactory lime status, and is moderately acid, but phosphate is as deficient as it is in the soils of subzone IA. There is potash deficiency in the lower, but is satisfactory in the upper, horizons of the soil, suggesting its organic origin.

(e) *Soils of subzone IE.* These can be defined as silt loams, and are throughout of the series of impeded drainage. Local areas of freely draining soils occur in the embanked and reclaimed area below Dolgarrog. Generally, the alluvium overlies a bed of peat which, in the area between the Porthllwyd and Afon Ddu, outcrops in a broad oval of a 100 acres; this has the features of a raised bog. Similar, but smaller outcrops, occur sporadically between Dolgarrog and Caerhun. Mineral soil overlying the peat varies in depth from a mere admixture with peat in the surface to a layer of approximately 91 cm. (3 ft.). The average depth is 30 cm. (1 ft.).

Table 9. *Soils of subzone IE*

A. Unembanked areas (below Tal-y-bont) periodically tidally flooded

Horizons (cm.)	Description of soil	Exchangeable	P ₂ O ₅	Exchangeable
		CaO (%)	(%)	K ₂ O (%)
(a) 0-20 (0-8 in.)	Brownish grey silty loam. Iron mottled	0.10	0.032	—
(b) 0-20 (0-8 in.)	Brownish grey silty loam. Iron mottled	0.11	0.021	—
(c) 0-15 (0-6 in.)	Brownish grey silty loam. Iron mottled	0.12	0.016	—
(d) 0-13 (0-5 in.)	Brownish grey silty loam. Iron mottled	0.10	0.027	—

B. Embanked areas (below Dolgarrog) seasonally flooded. Parent material is alluvium of the main Conway Valley

(a) 0-46 (0-18 in.)	Greyish silty loam, iron mottled (passing to peat)	0.05	0.0005	0.011
(b) 0-46 (0-18 in.)	Greyish silty loam, iron mottled (passing to peat)	0.07	0.0004	0.012
(c) 0-23 (0-9 in.)	Mixture of silty loam and peat (passing to peat)	0.07	0.0009	0.013
(d) 0-23 + (0-9 + in.)	Peat, friable, and free drainage	0.06	0.0008	0.015

The soils of the periodically tidally flooded area, between Porthllwyd and Caerhun, are not acutely deficient in lime and phosphate, but in the embanked areas these are more markedly deficient, particularly in phosphates (Table 9). This can be attributed to the more intense land utilization in the past of the latter areas, leading to a depletion of plant nutrients from the soil; with frequent tidal flooding there is some return of these nutrients to the soil.

The peat itself is distinctly acidic, which conforms with its 'raised' character.

(B) *The environmental factors of Zone II (pediment slope)*

The soils are primarily of colluvial origin, sedentary soils occurring locally, and their properties closely reflect the complex geological structure of the pediment slope. Five subzones are distinguished, and their environmental features are outlined in Table 10. Over the greater part of the zone the mean annual rainfall is undoubtedly greater than that of the adjacent lowlands. Thus, at Llanbedr-y-Cenin (155 m. (509 ft. o.d.)), the rainfall is 1540 mm. (60.63 in.) per annum.

Table 10. *The environmental factors of zone II*

Subzones ...	A	B	C	D	E
Range of mean annual rainfall (mm.)	1016-1524 (40-60 in.)	1270-1524 (50-60 in.)	1524 (60 in.)	1524 (60 in.)	1016 (40 in.)
Soil parent materials	Sedentary and colluvial rhyolitic rocks	Sedentary and colluvial pumice tuff, spilitic agglomerates, and dolerite	As for B with some glacial drift admixture	Sedentary and colluvial from slate	Sedentary and colluvial rhyolitic rocks with sand admixture
Tendencies in soil development	To podsolization (distinct podsoils present)	To brown earths	To brown earths	To podsolization	To podsolization
Topographical features	Steep pediment slopes	Steep pediment slopes with frequent terraces	Steep ravine slopes	Steep ravine slopes	Steep pediment slopes
Perviousness of parent material	Free drainage	Free drainage	Free drainage	Free drainage	Free drainage
Prevalence of soil series					
a_1	3	—	—	—	—
a_2	—	4	—	—	—
a_2-a_1	4	—	—	4	5
b	—	3	4	—	—
c_1	1	2	2	—	—
c_2		—	—	—	—
c_3		—	—	1	—
d_1		2	1	—	—
d_2		—	—	—	—
d_3		1	—	—	—
d_4		1	—	—	—

From Table 10 it is seen that the soils derived from acidic rocks are podsoils or show tendencies to podsolization.

Free-draining soils are preponderant throughout, though in the case of subzone IIB, some soils of impeded drainage occur, this being due to the prevalence of terraces in part of the subzone. The prominence of soils with equable moisture conditions in subzone IIC is a reflexion of its topographical situation, i.e. Dulyn Ravine, where high humidity and low light intensity undoubtedly prevail.

(i) *Distribution of subzones*

Subzones IIA and B are the most widely occurring, and they intermingle as a complex over the greater part of the zone. Thus subzone A occupies a considerable area of the west slopes of Conway Mountain, in Coed Dolgarrog, Ochr Gaer, and the lower slopes of Tal-y-Fan. Subzone B occurs primarily in Coed Dolgarrog, Allt Wyllt, and the lower slopes of Tal-y-Fan. (*Coed* = Wood.)

The topographical limits of the Dulyrn Ravine delimit subzones C and D. Finally, subzone IIE is localized on the north slopes of the Conway Mountain, where blown sand from the Conway estuary occurs as an admixture in the prevailing rhyolitic colluvial parent material of the soil.

(ii) *Summary of soil characteristics*

(a) *Soils of subzone IIA.* Within the zone of woodlands this subzone is unique in the presence of well-developed podsols. Such a soil is described in Table 11.

Table 11. *Soils of zone II*

Subzone IIA						
Horizons (cm.)	Description of soil	pH	Exchangeable CaO (%)	Organic matter (%)	P ₂ O ₅ (%)	Exchangeable CaO (%)
(a) Coetmor Woods, Conway, 122 m. (400 ft.) o.d. Drainage: free						
0-10 (0-4 in.)	Very dark peaty layer	3.80	0.10	—	0.0086	0.058
10-41 (4-16 in.)	Greyish gritty loam, very stony	3.60	0.04	—	0.0013	0.004
41-51 (16-20 in.)	Brown to rusty brown loam	3.97	0.02	—	0.0007	0.006
51-81 (20-32 in.)	Very tenacious material with brown, yellow and orange mottle	4.11	0.02	—	0.0006	0.005
81+ (32+ in.)	Very bouldery					
(b) Dolgarrog Woods, 76.25 m. (250 ft.) o.d. Drainage: free						
0-5 (0-2 in.)	Dull brownish grey loam with some organic material	4.09	0.024	13.12	0.00080	0.052
5-48 (2-19 in.)	Light brown loam	4.59	0.016	6.08	0.00028	0.010
48-74 (19-29 in.)	Dark brown loam	4.83	0.004	1.38	0.00052	0.005
Subzone IIB						
Coed Dolgarrog, 76.25 m. (250 ft.) o.d. Drainage: free						
0-15 (0-6 in.)	Dark brownish loam	5.28	0.384	8.76	0.00060	0.047
15-46 (6-18 in.)	Lighter coloured loam	5.45	0.156	5.88	0.00072	0.009
Subzone IIC						
(a) Dulyrn Ravine, 76 m. (250 ft.) o.d. Drainage: equable moisture conditions						
0-23 (0-9 in.)	Light brownish loam, very stony and bouldery	5.57	0.25	—	0.0019	0.009
(b) Dulyrn Ravine, 76 m. (250 ft.) o.d. Drainage: equable moisture conditions						
0-23 (0-9 in.)	As in (a) but soil slightly greyer	5.50	0.23	—	0.0098	0.004

This is distinctly podsollic in character, very acid, very lime and phosphate deficient, but not acutely deficient in potash. An example from Coed Dolgarrog (Table 11), with a similar plant nutrient status, is probably an eroded podsol in the initial stages of its redevelopment.

These apparently eroded podsols in this subzone are very prevalent; acidity in the probably residual B horizon varies from pH 4.29 to 4.83, and in the thin surface of raw humus from pH 4.09 to 4.29.

(b) *Soils of subzone IIB.* Soils which characterize this subzone are undoubtedly of a brown earth nature.

Lime and potash are not markedly deficient, the surface 15 cm. (6 in.) of soil having a higher concentration of these than deeper horizons (Table 11). This suggests the partly organic origin of these constituents in the surface soil. The soil is not acutely acid, the general range of acidity being pH 5.1-6.33.

In the pediment slopes below Tal-y-Fan the pumice tuff soils have a small admixture of dolerite, rhyolites, and slate in the parent material. Their presence, however, does not alter the general nature of the soils, and they are, therefore, classified with them.

Soils of impeded drainage are confined to the Allt Wyllt, on a succession of terraces. Their pH varies from 5.0 to 6.0.

This subzone is, therefore, distinguished by soils both of free and impeded drainage with a range of acidity, and lime status intermediate between those of IB and ID. When compared with IB, a distinctly lower phosphate status is shown to be present and is of a similar order to that of ID, IA and IIA.

(c) *Soils of subzone IIC.* The main parent materials of the subzone IIC are similar to those of IIB, but there is a small admixture of glacial materials similar to those of the drift emanating from the lateral valleys. These soils occur under environmental conditions of lower light intensity and higher humidity than those of IIA. The essential characters of the soils are summarized in Table 11.

The soils are similar to those of subzone IIB, differing only in their distinctly higher phosphate content, which may be due to the admixture of glacial material in their parent material.

(d) *Soils of subzone IID.* This subzone again occurs within the Dulyn Ravine, the slate parent material giving rise to a soil which is akin to that of subzone IA. A typical profile has a thin raw humus horizon (0–5 cm. (0–2 in.)) of pH 4.52 passing directly to a rusty brown loam soil (pH 4.60). As in the soils of IA, they may be brown earths showing a tendency to podsolization, or they may be in the first stages of the redevelopment of a podsol following erosion.

(e) *Soils of subzone IIE.* The soils of this subzone are similar to those of IIA, but tend to be sandy, as varying quantities of blown sand are present in the parent material. Distinct podsols are absent, apparently eroded profiles being present similar to the Coed Dolgarrog kind (Table 11).

(C) *The environmental factors of zone III (upland woodlands)*

Although the prevailing rainfall in this zone is high, marked tendency to podsolization is absent, except in the case of soils derived from rhyolite (Table 12). As in the lowland zone, soils of impeded drainage are most prevalent on the glacial drifts. There is a marked north to south gradient of rainfall, i.e. from approximately 1016–2032 mm. (40–80 in.), and the soils of impeded drainage tend to be more prevalent in the southern part of the zone.

(i) *Distribution of subzones*

Subzone IIIA dominates the greater part of the zone, occupying the flanks of the lateral valleys. All the other subzones occur sporadically in relation to rock outcrops of varying extent. A considerable part of the massive dolerite intrusion of Craig Eigiau is occupied by subzone IIIB. Subzone IIID occurs primarily in Sychnant area, with offshoots in the country between Llangelynin Old Church and Cae-côch. This area consists of a complex of subzones, comprising E, D and C (in order of prevalence).

(ii) *Summary of soil characteristics*

(a) *Soils of subzone IIIA.* The soils of subzone IIIA and IB are of common origin, but the former are developed under conditions of greater rainfall and cooler temperatures.

Table 12. *The environmental factors of zone III*

Subzones ...	A	B	C	D	E
Range of mean annual rainfall (mm.)	1270-1778 (50-70 in.)	1778-2032 (70-80 in.)	1270 (50 in.)	1016-1270 (40-50 in.)	1270 (50 in.)
Soil parent materials	Glacial drift of lateral valleys	Sedentary and colluvial from dolerite	Sedentary and colluvial from dolerite	Sedentary and colluvial from rhyolitic rocks	Sedentary and colluvial from pumice tuffs
Tendencies in soil development	To brown earths with some tendency to podsolization (?)	To brown earths with some tendency to podsolization (?)	To brown earths with some tendency to podsolization (?)	To podsolization	To brown earths (?)
Topographical features	Undulating flanks of lateral valleys	Slopes of outcrops	Slopes of outcrops	Slopes of outcrops	Slopes of outcrops with frequent terraces
Perviousness of parent material	Relatively impervious	Free drainage	Free drainage	Free drainage	Free drainage
Prevalence of soil series					
a_1	—	—	—	—	—
a_2	4	4	4	—	4
a_2-a_1	—	—	—	5	—
b	3	2	3	—	3
c_1	3	3	—	—	—
c_2	3	3	—	—	—
c_3	2	2	—	—	—
d_1	3	2	—	—	—
d_2	—	—	—	—	—
d_3	2	2	—	—	—
d_4	2	2	—	—	—

Table 13. *Soils of zone III*

Subzone IIIA					
Horizons (cm.)	Description of soil	pH	Exchangeable CaO (%)	P ₂ O ₅ (%)	Exchangeable K ₂ O (%)
(a) Hafoty Gwyn, Rowen, 265 m. (850 ft.) o.d. Drainage: free					
0-15 (0-6 in.)	Brownish grey loam	4.69	0.09	0.0015	0.030
15-66 (6-26 in.)	Greyish brown loam	—	—	—	—
66+ (26+ in.)	Greyish, very bouldery drift material	5.14	0.09	0.0047	0.005
(b) Lateral marine near Dulyň River, 305 m. (1000 ft.) o.d. Drainage: free					
0-23 (0-9 in.)	Greyish brown loam	5.55	0.21	0.0015	0.012
(c) Soglog area near Dulyň River, 274 m. (900 ft.) o.d. Drainage: seasonally wet					
0-20 (0-8 in.)	Dark brownish grey loam with slight iron mottle. Slight accumulation of humus at surface	4.83	0.10	0.0018	0.021
20-30 (8-12 in.)	Very stony grey loam	5.17	0.05	0.0042	0.002
30-51+ (12-20+ in.)	Very heavily iron mottled greyish loam	6.17	0.08	0.0022	0.004
(d) Bryn Gwenith, 274 m. (900 ft.) o.d. Drainage: seasonally wet					
0-15 (0-6 in.)	Greyish iron mottled loam	—	0.07	0.00119	0.007
15-91 (0-36 in.)	Light grey becoming heavily mottled with increasing depth	—	0.15	0.0187	0.004
(e) Soglog area, 274 m. (900 ft.) o.d. Drainage: permanently wet					
0-8 (0-3 in.)	Dark peaty material	5.04	0.78	0.0021	> 0.100
8-81 (3-32 in.)	Dark greyish brown fibrous peat	5.07	0.85	0.0023	0.102
(f) Soglog area, 274 m. (900 ft.) o.d. Drainage: permanently wet					
0-15 (0-6 in.)	Dark peaty soil	5.28	1.72	0.0045	0.225
15+ (6+ in.)	Light brown peaty soil	5.41	1.28	0.0059	0.320
(g) Soglog area, 274 m. (900 ft.) o.d. Drainage: permanently wet					
0-15 (0-6 in.)	Dark peaty material	5.51	1.05	0.0015	0.039
15+ (6+ in.)	Dark brown peaty material	5.41	1.24	0.0024	0.015
(h) Bron-y-Gader meadow, 274 m. (900 ft.) o.d. Drainage: permanently wet					
0-20+ (0-8+ in.)	Dark peaty material	6.20	> 0.80	0.0291	0.255
(i) White Hart, Rowen, 305 m. (1000 ft.) o.d. Drainage: seasonally wet (gley podsol)					
0-6 (0-2½ in.)	Raw amorphous black humus	4.00	—	—	—
0-13 (2½-5 in.)	Brownish grey with iron mottle	4.34	—	—	—
13+ (5+ in.)	Greyish brown loam with yellowish iron mottle	—	—	—	—

Thus, many of the characteristics of the soils of IB are evident here, as is seen in Table 13, which describes two soils developed under conditions of free drainage and equable moisture conditions.

Their acidity and plant nutritive status are similar to their equivalents in subzone IB. It is significant that these soils are not acutely base deficient (particularly site 1) at an altitude of 305 m. (1000 ft.), and this reflects their resistance to podsolization. The considerable phosphate reserve of the parent material is again evident. The satisfactory potash status of the surface soil suggests its organic origin, in view of its poverty in the deeper horizon.

These soil properties, other than hydrological conditions, persist in seasonally wet gleys (Table 13). The high phosphate content of the deeper horizons of the soil is again of interest.

Gley podsols are of local occurrence above the farm of Hafoty Gwyn (Rowen) (Table 13).

This type of soil has clearly a podsollic affinity, with a distinct surface raw humus horizon of considerable acidity. No podsols were, however, observed under conditions of free drainage.

Deep peats are the most prevalent of the permanently wet soils. They are highly humified, and putrefactive processes appear to be active within them. Their organic horizon may have incorporated in them varying quantities of mineral soil. Examples are given in Table 13.

These peaty soils are of moderate acidity, good to moderately deficient lime status: their phosphate content is not markedly deficient, and may be abundant. The very high potash content of some of these peats constitutes their outstanding feature. It is clear that these are not impoverished acid peats, and hence may be looked upon as transitional types between fen and acid peat (*Übergangsmoor*).

(b) *Soils of subzone IIIB*. This subzone occurs at a higher altitude and rainfall conditions than is normal for the zone of upland woodlands. Under such conditions podsols would be expected, but what are probably brown earths dominate the subzone. This may be accounted for by the basic nature of the dolerite parent material. Thus acidity is not marked, pH's of 5.22–5.24 and 5.32 being recorded from free-drainage sites.

(c) *Soils of subzone IIIC*. The soils of the subzone are similar in origin and characteristics to those of the foregoing subzone, but they occur under rainfall conditions of 1270 mm. (50 in.) per annum, at an altitude of 244–305 m. (800–1000 ft.).

(d) *Soils of subzone IIID*. As in the pediment slopes the soils derived from rhyolitic rocks show a tendency to podsolization, but no intact podsols were observed, as undisturbed woodlands are absent. Rusty brown loam soils with surface raw humus are prevalent, and probably represent eroded podsols in the initial stages of redevelopment. Acidity is marked, ranging from pH 3.95 in a shallow skeletal soil of high organic matter content developed from scree material to pH 4.2 in the first 15 cm. (6 in.) of a rusty brown soil. Acidity, therefore, is of a similar order to that of subzone IIB.

(e) *Soils of subzone IIIE*. Brownish loams, apparently non-podsolized, are similar to their equivalents in the pediment slopes, in that their range of acidity is of the order of pH 5.6–5.7; these were recorded in the surface 15 cm. (6 in.) of two typical sites.

(D) *The environmental factors of zone IV (Ulex gallii acidic grasslands with heath)*

An analysis of the environmental factors of the zone is tabulated in Table 14.

Table 14. *The environmental factors of zone IV*

Subzones ...	A	B	C	D	E	F	G	H
Range of mean annual rainfall (mm.)	1016-1270 (40-50 in.)	1270 (50 in.)	1270-1778 (50-70 in.)	1397-1778 (55-70 in.)	1651-2032 (65-80 in.)	1397-1778 (55-70 in.)	1524-1651 (60-65 in.)	2032 (80 in.)
Soil parent materials	Sedentary and colluvial from rhyolitic rocks	Mixed colluvium of acidic and basic rocks	Mixed colluvium of acidic and basic rocks	Glacial drift of lateral valleys	Glacial drift of lateral valleys	Glacial drift of lateral valleys with much acidic rocks	Glacial drift of lateral valleys	Sedentary and colluvial from dolerite
Tendencies in soil development	To podsols	To podsols	To podsols	To podsols	To podsols	To podsols	To podsols	To brown earths (?)
Topographical features	Crests and flanks of ridges	Crests and flanks of ridges	Upper slopes of lateral valleys	Slopes of lateral valleys	Slopes of lateral valleys	Slopes of lateral valleys	Slopes of lateral valleys	Flank of dolerite outcrop
Perviousness of parent materials	Free drainage	Free drainage	Free drainage	Relatively im-pervious	Relatively im-pervious	Relatively im-pervious	Relatively im-pervious	Free drainage
Prevalence of soil series								
a_1	4	4	2	1	1	—	—	—
a_2	—	—	—	—	—	—	—	5 (?)
a_2-a_1	4	4	3	1	2.5	—	3	—
b	—	1	2	2.5	2	1 (?)	—	—
c_1	—	—	3	3	2	1	4	—
c_2	—	—	—	3	2	3	2	—
c_3	—	2	4	3	3.5	4	1	—
d_1	—	1	—	1	2	3.5	—	—
d_2	—	—	—	—	—	—	—	—
d_3	—	—	—	2	2	2	1	—
d_4	—	—	—	2	1	1	—	—

Podsolization is general, and this tends to obscure the effect of parent material on the course of soil development more than in the preceding zone. There are, however, some discernible effects of the bearing of parent materials on soil properties. At the extreme annual rainfall of 2032 mm. (80 in.), where normally podsolis would be expected, the dolerite soils show a marked resistance to podsolization, as in the zone of upland woodland.

Free-draining podsolis are developed from the colluvial and sedentary parent materials of the lower rainfall northern part of the district; while in the higher rainfall southern part, gley podsolis and soils of impeded drainage are more prevalent in relation to all kinds of parent materials other than dolerites.

Soils derived from similar parent materials, but developed under contrasting climate conditions, are relegated to different subzones, and in this manner, subzones A from C, and D and E from G are differentiated from each other.

(i) *Distribution of subzones*

Subzone IV A extends from the southern flank of Talyfan along the ridge of Cefn Maen Amor to Maen Esgob. Northwards from the latter point extends subzone B, incorporating the Sychnant area and Conway Mountain. Subzone IV C has a more southern distribution, occurring above the glacial drift on the flanks of the lateral valleys from the southern slopes of Talyfan to Waen Bryn Gwenith. The lateral valley of the river Tafolog incorporates subzones IV D and F, while that of the Porthllwyd-Dulyn rivers includes E and G. Subzone IV H is localized in a small area on the southern colluvial flanks of Craig Eigiau.

(ii) *Summary of soil characteristics*

(a) *Soils of subzone IV A.* Free-draining podsolis, shallow and locally skeletal, are the prevailing soil type, but much erosion of them has occurred, giving rise to rusty brown residual soils. A typical non-eroded soil is described in Table 15.

Acidity is high, lime and phosphate are very deficient, but potash is satisfactory, particularly in the A_0 horizon where it is clearly of organic origin. The acidity of the eroded soils is slightly lower, varying from pH 4.03 to 4.6 in the surface 15 cm. (6 in.).

(b) *Soils of subzone IV B.* In general features the soils are similar to those of the foregoing subzone. A non-eroded profile (Table 15) differs significantly from the podsol of subzone IV A in the following features: (1) the potash status of the podsol of subzone IV B is lower than that of IV A, though this element is not acutely deficient; (2) the organic matter content of the A_0 horizon is markedly less in this profile.

The eroded soils do not differ markedly in their acidity from the non-eroded. A range of pH from 3.8 to 4.35 was recorded in the surface 15 cm. (6 in.). A similar acidity was found in gley podsolis which occur occasionally (e.g. A_0 pH 3.93, A-G pH 4.78).

(c) *Soils of subzone IV C.* Here, under conditions of higher rainfall, gley podsolis become the most prevalent soil series, but for direct comparison a free-draining podsol is described (Table 15). In acidity and nutrient status it is essentially similar to the podsol of the foregoing subzone. The organic matter content is high and is of the same order as that of the podsol of IV A in the A_0 horizon, but in the succeeding horizons the soil of IV C has a distinctly higher organic matter content. This is probably related to the higher rainfall of this subzone. The widely occurring gley podsolis have a slightly lower acidity than those of the free-draining podsolis (e.g. A_0 pH 4.0, A-G pH 4.54), while a seasonally wet gley had a pH of 5.03 in surface 15 cm. (6 in.) of soil.

(d) *Soils of subzone IVD.* Uneroded podsoles are but of local occurrence, since soils of impeded drainage prevail. A free-draining podsol is described in Table 16.

This soil differs from the foregoing podsoles in the following important features: (1) its exchangeable CaO content is at least twice that of the soils of subzones IVA, B and C; (2) it has a distinctly high potash content; (3) the soil is generally of a high organic matter content, though slightly lower than subzones IVA and C.

The high acidity of this profile is not general in others examined in this subzone, e.g. another similar podsol has the following pH range of A_0 pH 4.04, A pH 4.75, B pH 4.30. In the case of an apparently eroded profile, the acidity range in the surface 15 cm. (6 in.) of soil is from pH 4.20 to 4.71. Non-podsolized, rusty brown soils of equable moisture

Table 15. *Soils of zone IV*

Horizons (cm.)	Description of soil	pH	Organic matter (%)	Exchangeable CaO (%)	P ₂ O ₅ (%)	Exchangeable K ₂ O (%)
Subzone IVA						
Near summit of Conway Mountain, 244 m. (800 ft.) o.d. Drainage: free						
0-9 (0-3½ in.)	Dark organic layer with some mineral admixture	3.83	31.76	0.128	0.00692	0.092
9-23 (3½-9 in.)	Light grey gritty stony loam (locally darker with humus stains)	3.81	4.224	0.040	0.00088	0.018
23-38 + (9-15 + in.)	Dull rusty brown stony loam	4.36	5.408	0.020	0.00028	0.012
Subzone IVB						
Quarry slopes of Cefn Maen Amor, 305 m. (1000 ft.) o.d. Drainage: free						
0-8 (0-3 in.)	Black fibrous to greasy textured organic layer with some mineral admixture	3.76	16.8	0.028	0.00168	0.035
8-14 (3-5½ in.)	Dull brownish grey loam with faint iron mottle	4.16	5.47	0.012	0.00036	0.009
14-25 (5½-10 in.)	Bright rusty brown light stony loam	4.54	4.704	0.032	0.00020	0.009
25 + (10 + in.)	Light greyish brown loam with much disintegrating rock	4.64	2.304	0.012	0.00028	0.004
Subzone IVC						
South-western slope of Pen-y-Gader, 458 m. (1500 ft.) o.d. Drainage: free						
0-8 (0-3 in.)	Dark amorphous organic layer	3.98	32.8	0.092	0.00536	0.140
8-25 (3-10 in.)	Dark greyish loam with some organic matter. Faint iron mottle	4.05	16.16	0.024	0.00600	0.031
25 + (10 + in.)	Stony dull light brown loam	4.55	9.52	0.016	0.00028	0.005

conditions occur more extensively than the free-draining series. They are distinctly less acid, and have an acidity range of pH 4.47-5.15 in the first 15 cm. (6 in.) of soil.

Soils of impeded drainage are generally less acid, e.g. seasonally wet gley pH 5.24-6.02, deep peat pH 4.00-5.5 (the higher figure occurring in a flush).

(e) *Soils of subzone IVE.* Only one free-draining podsol site was observed in this subzone, which is described in Table 16.

Although this soil is derived from the same parent materials as those of subzone IVD, there are distinct contrasts in their plant nutrient status. Thus E is more markedly deficient in all plant nutrients and its organic matter content is also less. Acidity generally in this subzone is of the same order as that in subzone IVD. Thus, apparently eroded podsoles have a pH range of 3.9-4.37 in the surface 15 cm. (6 in.) of soil. Gley podsollic soils are

similar in acidity to the podsol of Table 16, e.g. A_0 pH 4.31, $A-G$ pH 4.23, B pH 4.78. Seasonally wet gleys vary considerably in acidity from pH 4.39 to 6.78. Acidity is high in seasonally wet peaty gleys, e.g. pH 4.31 in the peaty horizon, and 4.78 in the gleyed soil below. Deep peats are distinctly acid, the range of pH being 3.98–4.78.

The higher rainfall that is probably prevalent over subzone IVE may in part account for the lower nutrient status of its soils when compared with those of subzone IVD. On the other hand, differences may exist in the parent materials of the soils, the determination of which is beyond the scope of the present investigations (e.g. mineralogical examination of the soil).

Table 16. *Soils of subzone IV*

Horizons (cm.)	Description of soil	pH	Organic matter (%)	Exchangeable CaO (%)	P ₂ O ₅ (%)	Exchangeable K ₂ O (%)
Subzone IVD						
Tal-y-Braich, Bwlch-y-Ddeufaeh, 366 m. (1200 ft.) o.d. Drainage: free						
0-5 (0-2 in.)	Dark amorphous greasy organic layer	3.70	28.00	0.132	0.00428	0.124
5-20 (2-8 in.)	Dull brownish grey loam	3.78	11.28	0.068	0.00088	0.047
20-38 + (8-15 + in.)	Rusty brown very stony and bouldery	3.95	5.52	0.044	0.00036	0.023
Subzone IVE						
Near Hafod-y-Gorswen, 336 m. (1100 ft.) o.d. Drainage: free						
0-6 (0-2½ in.)	Dark amorphous organic layer	4.25	20.00	0.108	0.00888	0.098
6-23 (2½-9 in.)	Brownish grey to locally grey loam	4.27	7.36	0.012	0.00044	0.009
23-33 (9-13 in.)	Light rusty brown loam	4.57	3.24	0.012	0.00012	0.003
33-48 + (13-19 + in.)	Light greyish brown loam with yellowish tinge	4.80	2.29	0.012	0.00028	0.003
Subzone IVF						
Calluna area near River Tafolog, 336 m. (1100 ft.) o.d. Drainage: seasonally wet (gley podsol)						
0-13 (0-5 in.)	Dark fibrous organic layer	3.69	32.24	0.048	0.00252	0.082
13-23 (5-9 in.)	Dark brownish grey compact loam	3.67	11.92	0.024	0.00088	0.009
23-38 (9-15 in.)	Dark rusty brown loam	4.37	7.76	0.008	0.00028	0.009
38-58 (15-23 in.)	Brownish grey iron mottled loam	4.46	2.32	0.008	0.00028	0.006
58-71 + (23-38 + in.)	Greyish loam heavily iron mottled	4.68	1.56	0.012	0.00028	0.003
Subzone IVG						
South-west of Bwlch-y-Gaer, 366 m. (1200 ft.) o.d. Drainage: free						
0-5 (0-2 in.)	Dark greyish black organic layer	4.27	18.56	0.072	0.00220	0.082
5-25 (2-10 in.)	Dull rusty brown stony loam	4.33	10.24	0.036	0.00060	0.031
25-41 + (10-16 + in.)	Lighter coloured loam	4.76	6.00	0.020	0.00028	0.012
Subzone IVH						
South-west end of Craig Eigiau, 397 m. (1300 ft.) o.d. Drainage: free						
0-23 (0-9 in.)	Dark greyish brown loam	5.05	14.96	0.128	0.00052	0.030
23-38 + (9-15 + in.)	Dark brownish to rusty brown loam	5.21	5.28	0.036	0.00020	0.005

(f) *Soils of subzone IVF.* No soils of free drainage occur within this subzone, hence a gley podsol is described (Table 16).

Acidity and plant nutrient status are of a similar order to the podsol of subzone IVE, but it is distinctly more lime and potash impoverished than the podsol of subzone IVD.

The organic matter content of the various horizons approaches that of the podsol of subzone IVC, and is thus higher than that prevalent in the other soils derived from glacial

drift. The differences between the soils, described in subzones D and F respectively, can be attributed to the contrasts in the base reserves of their parent materials, those of D being greater than those of F. This is also reflected in the acidity range of other soil series. A seasonally wet peaty gley had a range of pH from 4.22 to 4.37, while deep peats have a distinctly low pH, i.e. from 3.72 to 4.37. These acidity ranges approach those of subzone IVE, but are clearly higher than those of IVD.

(g) *Soils of subzone IVG.* No podsoles exist in this subzone, but a free-draining soil is described above (Table 16).

No distinct A horizon is present. The surface organic layer is in the nature of acid raw humus. Thus the profile may be an eroded podsol in the initial stages of redevelopment, or a weakly podsolized brown earth. Lime deficiency is not as great as in the immediately adjacent subzone E, and approaches that found in IVD.

Potash is plentiful, and much of it in the surface horizon appears to be of organic origin. Phosphate is deficient, while the organic matter content is much lower than that met with in the podsoles of subzones IVE, D and F. Acidity in the first 15 cm. (6 in.) of mineral soil, in sites similar to that described above, varies from pH 3.86 to 4.78. The range of seasonally wet gleys is from pH 4.93 to 5.74, and in peaty gleys from pH 4.41 to 4.54 in the organic horizon. The higher lime status and lower acidity of the soil of subzone IVG, when compared with that of the adjacent IVE, can be attributed to differences in rainfall, as the two are of common origin.

(h) *Soils of subzone IVH.* The basic character of the parent material of the soil is reflected in the general absence of podsoles. A probable brown earth profile is described in Table 16.

Acidity is not marked and reflects the absence of extreme lime deficiency in the soil. The probable organic origin of the potash is again evident in the surface horizon. Phosphate is acutely deficient. This subzone occurs under rainfall conditions of approximately 2032 mm. (80 in.) per annum at an altitude of 381 m. (1250 ft.) and 427 m. (1400 ft.). It is clear, therefore, that dolerite soils have a considerable resistance to podsolization.

(E) *The environmental factors of zone V (valley peats)*

Throughout the zone the rainfall is at least 2032 mm. (80 in.) per annum. The zone occupies the flanks of the inner reaches of the lateral valleys on gentle to moderate slopes. Usually the soils are derived from glacial drift, and the series of impeded drainage are most frequent. An analysis of the environmental factors of the zone is set out in Table 17.

The abundance of deep peats is clearly evident. The average depth of peat is 61 cm. (2 ft.) and does not exceed 91 cm. (3 ft.). They are peat gleys in nature, dependent on both telluric and orographic moisture for their formation, as opposed to peat podsoles in the succeeding zone of blanket peat. Free-draining podsoles are generally rare. There is an abundance of gley podsoles in subzone VA, though they are not prevalent elsewhere. The parent materials of the soils have no significant effect on the course of soil development. Thus, in subzone VD, occurring in relation to dolerites, there is the same prevalence of peats as in other subzones. Subzone VC is a possible exception where brownish non-podsolized soils are prevalent in relation to the alluvial parent material.

Rainfall is of a similar order throughout the zone except in the case of subzone VF, which occurs at a lower altitude, and probably has a lower rainfall. This is reflected in the

Table 17. *The environmental factors of zones V and VI*

Subzones ...	A	B	C	D	E	F	Zone VI
Range of mean annual rainfall (mm.)	2032 (80 in.)	2032 (80 in.)	2032 (80 in.)	2032 (80 in.)	2032 (80 in.)	1778-2032 (70-80 in.)	> 2032 (> 80 in.)
Soil parent materials	Glacial drift of lateral valleys	Glacial drift of lateral valleys	Alluvium over peat	Sedentary and col-luvial from dolerite	Glacial drift of lateral valleys	Glacial drift of lateral valleys	Ordovician sedi-mentary and volcanic rocks
Tendencies in soil development	To gley podsoils and deep peat gleys	Raised peat (north moor)	To gley soils	To gley podsoils and deep peats	Deep peat gleys	Shallow and deep peaty gleys	Deep peat podsoils
Topographical features	Undulated flanks and bottoms of lateral valleys	Flat river margins	Flat river margins	Outcrops with frequent terraces	Flat to gently sloping	Flat to gently sloping	Mature rounded locally sharp in relation to vol-canic rocks
Perviousness of parent material	Relatively im-pervious	?	?	Free drainage	Relatively im-pervious	Relatively im-pervious	—
Prevalence of soil series							
a_1	1.5	—	—	2.5	—	—	2.5
a_2	—	—	—	—	—	—	2
a_2-a_1	1	—	—	—	—	—	—
b	2.5	—	3	—	—	1.5	1
c_1	2	—	3	—	—	3	—
c_2	2.5	1	2	2	1.5	4	3
c_3	4	—	—	2.5	1	1.5	4
d_1	4.5	4	—	3.5	4.5	4	4.5
d_2	2	3	—	4	3.5	—	2.5
d_3	1	1	—	—	—	2.5	1
d_4	—	—	3	—	—	1	—

greater prevalence of seasonally wet soils within it, in spite of its very gently sloping topography.

(i) *Distribution of subzones*

All the flanks of the main lateral valleys are occupied by subzone VA. The other subzones are more localized, particularly, B and C occurring marginal to streams in the Eigiau and Dulyn Valleys. The dolerite outcrop of Cerrig Cochion, in the lower reaches of the Dulyn Valley, comprises subzone D. Subzones E and F occupy the flat expanse of country from Cwm Eigiau to Waen Bryn Gwenith, the former occupying a limited area near the lake and the latter extending from thence to Waen Bryn Gwenith.

(ii) *Summary of soil characteristics*

(a) *Soils of subzone VA.* Free-draining podsols are but local in occurrence, and the acidity of the soil is similar to that found in equivalent profiles in zone IV (Table 18).

Table 18. *Soils of zone V*

Horizons (cm.)	Description of soil	pH
Subzone VA		
(a) Lower slopes of Y Drosgl, 397 m. (1300 ft.) o.d. Drainage: free		
0-15 (0-6 in.)	Dark loose dry humus	3.93
15-41 (6-16 in.)	Brownish grey light loam	4.13
41-61 (16-24 in.)	Rusty brown loam	4.47
61+ (24+ in.)	Greyish glacial drift (shales, slates, and volcanic rocks)	—
(b) Dulyn Valley, 534 m. (1750 ft.) o.d. Drainage: seasonally wet		
0-18 (0-7 in.)	Raw amorphous black peaty material	3.84
18-27 (7-10½ in.)	Greyish loam with diffuse iron mottle	4.29
27-47 (10½-18½ in.)	Deep rusty brown layer, strongly iron mottled with local humus stains	4.32
47+ (18½+ in.)	Shale colluvium	—
Subzone VE		
Near Llyn Eigiau, 381 m. (1250 ft.) o.d. Drainage: permanently wet		
0-80 (0-36 in.)	Peat (Betula remains at base)	3.76-4.27
80-128 (36-46 in.)	Grey loam, iron mottled, with some plant remains (twigs)	—
128+ (46+ in.)	Grey indurated glacial drift (slates, shales and volcanic rocks) very bouldery	—
Subzone VF		
Near Trosbwl, Porthllwyd River, 357 m. (1150 ft.) o.d. Drainage: seasonally wet		
0-25 (0-10 in.)	Peaty horizon	3.86
25-41 (10-16 in.)	Humus stained medium loam with diffuse iron mottle	—
41-64 (16-25 in.)	Brownish grey medium loam with diffuse iron mottle	4.44
64+ (25+ in.)	Grey indurated glacial drift (slates, shales, and volcanic rocks)	4.47

Gley podsollic soils are abundant on the south side of the Dulyn Valley, their acidity being of similar order to that of free-draining podsols, e.g. *A*₀ pH 3.84, *A-G* pH 4.29, and *B* pH 4.32. Seasonally wet gleys and peaty gleys are less acid, e.g. a gley had a pH of 5.5 in the surface 15 cm. (6 in.) of soil, and the peaty horizon in peaty gleys varies in pH from 4.19 to 4.27.

In the troughs of undulations there is frequently a tendency to raised peat development, its depth being approximately 91 cm. (3 ft.), acidity in such areas being below pH 4 (i.e. from pH 3.68 to 3.89). Peats of about 61 cm. (2 ft.) in depth are more widespread. Occurring on gentle slopes, they show no tendency to raised growth, and are generally wetter. Their acidity is above pH 4 (pH 4.19-4.27). Flushes traverse the peats sinuously,

often skirting the margin of raised peat areas. The soils of the flushes are usually permanently wet shallow peaty gleys, acidity varies from pH 4.2 to 4.34 in the peaty horizon.

(b) *Soils of subzone VB.* The soils are predominantly raised peats and their acidity is similar to that in the foregoing subzone. Thus in Cwm Eigiau, pH of 3.65 in the central *Calluna* area, and 5.12 in the marginal flush were recorded.

(c) *Soils of subzone VC.* The soils are of a silty loam character. No pH determinations were made on these soils, but they clearly will be less acid than in the foregoing subzones.

(d) *Soils of subzone VD.* On the dolerite outcrops free-draining and gley podsols are prevalent while the terraces are dominated by deep peats which show raised peat features and are characterized by *Calluna* vegetation. Acidity in the first 15 cm. (6 in.) of these peats varies from pH 3.87 to 4.27.

(e) *Soils of subzone VE.* The soils of this subzone are common to those of subzone VA in their origin, but in VE deep peats are more widespread and attain a greater average depth. The peats are usually about 91 cm. (3 ft.) in depth, but frequently attain 152 cm. (5 ft.). The acidity of these peats varies from pH 3.76 to 4.27, and in a local flush a pH of 6.4 was recorded. Free-draining soils are absent and gley podsols are rare.

(f) *Soils of subzone VF.* With lower altitude, and probably lower rainfall in the country between Llyn Eigiau and Waen Bryn Gwenith, subzone VE merges into F. Seasonally wet peaty gleys become very abundant, and the deep peats progressively shallower. The latter are distinctly acid, ranging in pH from 4.16 to 4.62, while in flushes it varies from pH 5.27 to 6.4. Acidity in the seasonally wet peaty gleys is of a similar order (Table 18). Marginal to the River Porthllwyd these soils have a higher pH of up to 5.13. The seasonally wet gleys also found marginal to the Porthllwyd have a pH of 5.16. Marginal to this river a narrow band of equally moist brown soil occurs, of pH 4.77. Thus, compared with the soils of the other subzones, we have here a range of types which are less distinctly acid.

(F) *The environmental factors of zone VI (blanket peats)*

The prevailing high rainfall and low temperatures are the dominating factors in soil formation within this zone, such that no evidence of the differentiating effect of the various parent materials on the course of soil development is available; therefore, no subzones are recognized. The environmental factors prevailing in this zone are outlined in Table 17.

(i) *Distribution and summary of soil characteristics*

The blanket peat is essentially a peat podsol, and it attains its maximum development on the Gledr Ffordd, where peat depths of 183 cm. (6 ft.) are common. On the Foel Fras, though it is of extensive occurrence, it but occasionally exceeds a depth of 76 cm. (2½ ft.). In the Drosgl-Drum-Foel Lwyd area, depths of 91–122 cm. (3–4 ft.) are common, locally attaining 183 cm. (6 ft.). Peat is but weakly developed on Tal-y-Fan, where it does not exceed a depth of 43 cm. (1½ ft.) on the narrow summit ridge.

In the drier peats the pH's range from 3.44 to 3.90, while on wetter situations they vary from pH 4.00 to 4.40. Such a peat is described from the Drosgl slopes (Table 19).

Robinson & Wasowicz (1935) describe a similar profile from the Foel Fras area, where a pH of 3.88 was recorded from the *A* horizon and 4.47 for the *B* horizon. Only traces of lime were found in the profile.

The erosion of these peats is not of uniform intensity. The greatest intensity is found

on the Gledr Ffordd, and the least on the Foel Fras, while intermediate conditions exist in the Drosgl-Drum-Foel Lwyd and Tal-y-Fan areas. Gley podsollic soils are frequent, and an instance is described below from the upper slopes of the Drum. In spite of the shallowness of the soil there are indications of drainage impedance. Such soils are very frequent on the upper slopes of Y Foel Fras, where the depth of the organic horizon may attain 30 cm. (1 ft.).

Shallow seasonally wet peaty gleys are frequent in hollows, the acidity of the organic horizon varying from pH 3.76 to 4.84. Free-draining soils of the summits are of a skeletal nature, and typical examples are described in Table 19.

Table 19. *Soils of zone VI*

Horizons (cm.)	Description of soil	pH
(a) Slopes of Y Drum, 610 m. (200 ft.) o.d. Drainage: permanently wet		
0-183 (0-72 in.)	Fibrous peat	3.44
183-198 (72-78 in.)	Grey loam (upper 8 cm. (3 in.) humus stained)	4.00
198+ (78+ in.)	Rusty brown loam with much disintegrating rock	4.37
(b) Slopes of Y Drum, 610 m. (200 ft.) o.d. Drainage: seasonally wet		
0-10 (0-4 in.)	Very dark amorphous organic horizon	3.75
10-17 (4-6½ in.)	Greyish stony loam	—
17-22+ (6½-8½+ in.)	Rusty brown very strongly iron mottled loam passing to disintegrating rock	4.23
(c) Near summit of Y Drum, 771 m. (2528 ft.) o.d. Drainage: free		
0-8 (0-3 in.)	Greasy amorphous organic layer	3.93
8-18 (3-7 in.)	Very stony greyish mineral soil passing to disintegrating rock	3.93
(d) Near summit of Y Foel Fras, 942 m. (3090 ft.) o.d. Drainage: free		
0-15 (0-6 in.)	Mixture of mineral soil, much stones, and organic material passing directly to disintegrating rock	4.23

Erosion of these shallow soils is active, particularly in the Foel Lwyd area, where a pH of 4.27 was recorded in the residual mineral soil.

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AN EXAMPLE OF SUDAN ZONE VEGETATION IN NIGERIA

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I. INTRODUCTION

Popular notions about the vegetation of the northern boundary of Nigeria vary greatly. Some people imagine that the whole of Nigeria is covered by rain forest, while others have heard about the 'encroaching Sahara' and assume that the northern boundary must be a barren waste, with only a few thorny trees (or even cacti!), about to be engulfed in desert. There has been wide interest in the alarmist views of Stebbing (1935), who toured West Africa in 1934, and maintained that the Sahara would shortly overwhelm much of northern Nigeria. Less is heard of the Anglo-French Commission of 1936-7 which visited parts of Niger Colony and Nigeria, and concluded that Stebbing's extreme views were quite unjustified. Members of this Commission included in their reports [Nigerian Government Sessional Paper no. 37 (1937); Collier & Dundas (1937); see also Aubreville (1937)] brief descriptions of the vegetation, and Fairbairn (1939, 1943) has attempted a more ambitious classification. These reports show that vegetation near the northern boundary of Nigeria is neither rain forest nor semi-desert, but is a dry type of savanna woodland and scrub. The field work upon which these reports were based consisted almost entirely of travel observations, and Champion, in a preface to one of Fairbairn's papers (1943), rightly points to the need for determining the ecological status of the communities which have been described as formations and associations. Detailed work has been done in similar parts of French West Africa (e.g. Trochain, 1940) but not in British colonies.

French workers have followed Chevalier (1900, 1933) and others in describing the savanna vegetation of West Africa in relation to three broad zones which lie more or less parallel to the Equator between the Equatorial Forest and the Sahara. These zones were named by Chevalier: *Zone Sahélienne*, *Zone Soudanienne* and *Zone Guinéenne*.^{*} This zonation has been used in a brief outline of Nigerian vegetation recently published (Keay, 1949). This account is based on ecological surveys in selected localities within each zone, integrated by travel observations. The present paper is an account of work done in the Zamfara Forest Reserve, near Zurmi, Sokoto Province (see Fig. 1), in a locality typical of the Sudan zone.

The greater part of the Zamfara Forest Reserve is occupied by open savanna woodland. Several distinct communities are at once evident, but there is no obvious correlation between vegetation and topography, except on rocky slopes and by water-courses. Practically all the vegetation has been influenced by cultivation and habitation, but during the last 80 years or so grass fires and cattle have probably been the main controlling factors. The vegetation was found to be a complex mosaic of seral communities, at different stages of development and influenced by different biotic factors or combinations of factors, superimposed on a mosaic of several soil types.

The concepts of the *association-segregate* (Braun, 1935) and the *topographical catena* (Morrison, Hoyle & Hope-Simpson, 1948) proved valuable in the interpretation of this bewildering vegetation. The problem of determining the climatic climax is by no means easy, but vegetation on low rocky hills suggests an answer which is corroborated by observations in other parts of Africa. The climax in the Sudan zone appears from this evidence to be deciduous woodland with a dense understory of deciduous erect and scandent shrubs and only occasional patches of grass. Biotic influences have turned this

^{*} It is generally agreed that these zones, which have their counterparts in other parts of Africa, may be distinguished roughly as follows:

Sahel zone ('Zone des steppes sahéliennes ou des épineux', Chevalier (1933)). Mean annual rainfall: 250–500 mm. Rainy months (> 2 cm.): 4 to 5. Trees: usually less than 10 m. high, mostly fine-leaved and thorny; deciduous, not forming closed canopy; typical species are *Acacia raddiana*, *A. senegal* and *Salvadora persica*. Herb stratum: discontinuous or annual, dominated by grasses less than 1 m. high; grass fires consequently less fierce compared with the other zones. Streamside vegetation: trees and shrubs of the Sudan zone forming deciduous thickets and tangles with occasional large trees (to 15 m.).

Sudan zone ('Zone soudanaise proprement dite ou de la brousse parc', Chevalier (1933)). Mean annual rainfall: 500–1000 mm. (Chevalier puts the southern limit at 1500 mm.). Rainy months (> 2 cm.): 5 to 6. Trees: usually up to about 15 m. high, often less, but sometimes to 18 m., or even more, by water-courses; fine-leaved and broad-leaved trees in roughly equal proportions, with a fair number of thorny species; mostly deciduous; sometimes forming a closed canopy; typical species are *Sclerocarya birrea*, *Lannea microcarpa*, *Piliostigma reticulatum* and *Albizzia chevalieri*. Herb stratum: continuous, dominated by perennial grasses from 1 to 1.5 m. high; grass fires fiercer and more frequent than in Sahel zone. Streamside vegetation: deciduous thickets and tangles with larger trees (riparian woodland).

Guinea zone ('Zone guinéenne ou des savannes sub-forestières avec galeries', Chevalier (1933)). Mean annual rainfall: 1000–1500 mm. or more in certain areas. Rainy months (> 2 cm.): 7 or 8. Trees: usually up to about 18 m., often less, but up to 30 m. or more in *forest outliers* (see Keay, 1947); mostly broad-leaved, fine-leaved and thorny trees being rare; deciduous but often for quite short periods only; forming a more or less closed canopy wherever there is protection from fire and farming; typical species are *Isobertinia doka*, *Monotes kerstingii*, *Daniellia oliveri* and *Lophira alata*. Herb stratum: continuous, dominated by perennial grasses from 1.5 to 3 or even 4 m. high; grass fires normally fierce and annual. Streamside vegetation: *forest outliers*, with an evergreen understory. The Guinea zone is wide and variable. Aubreville (1936) recognizes several districts, and in Nigeria the zone is divided into northern and southern subzones. To the south of the Guinea zone lie the Forest Regions.

into open savanna with grass dominant below widely spaced trees. It is, however, quite possible that these influences are so ancient and widespread that the climax has never been able to develop properly during the present climatic era.

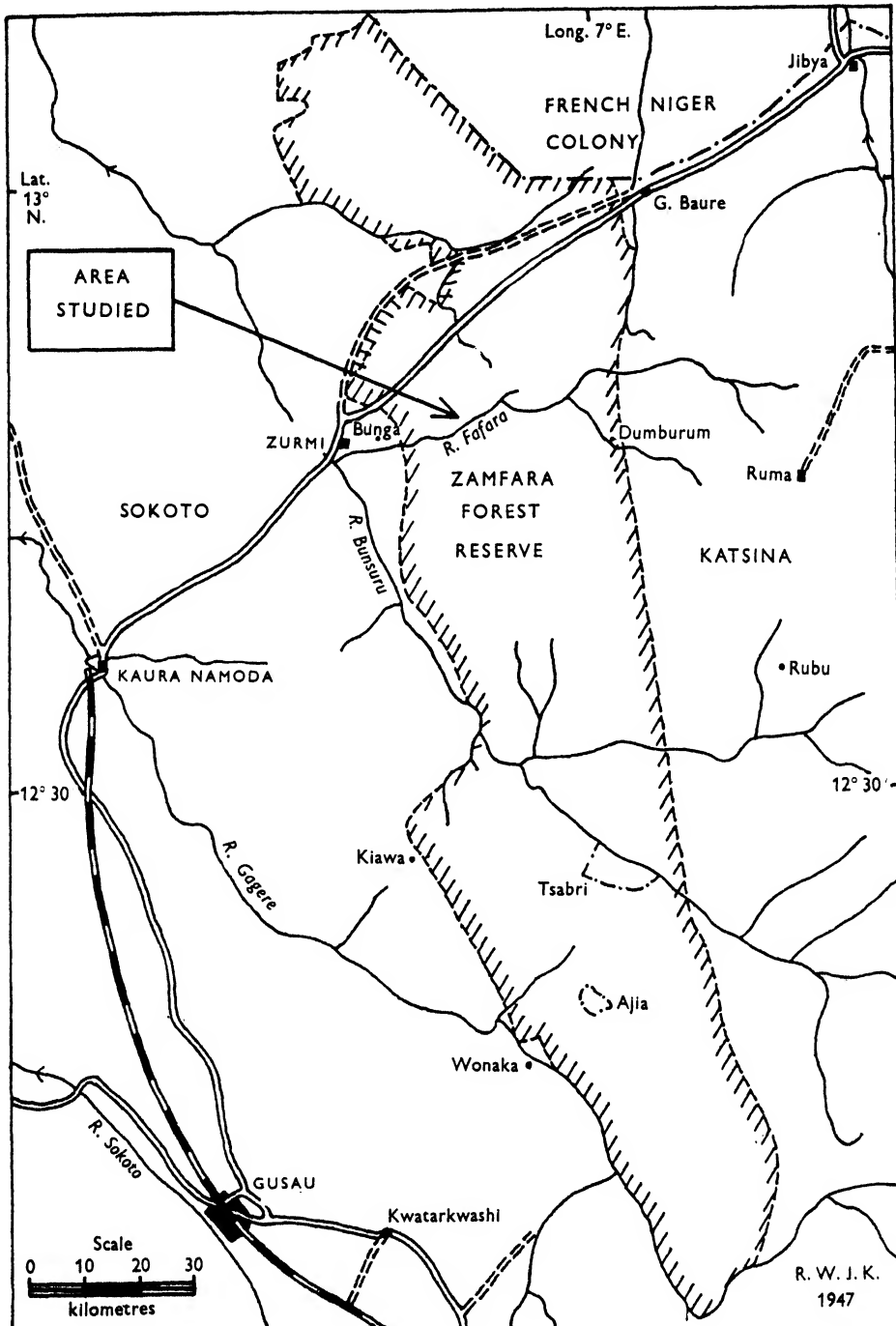


Fig. 1. Map showing Zamfara Forest Reserve and the area studied.

II. DETAILS OF THE ZURMI AREA

Position

The Zamfara Forest Reserve is in the north-eastern part of Sokoto Province and lies between latitudes 12 and 13° N. and on longitude 7° E. (see Fig. 1). It has an area of about 240,000 ha. and is roughly rectangular in shape. The eastern boundary of the reserve is the boundary between Sokoto and Katsina Provinces; another large reserve in Katsina is contiguous with it.

The ecological work was done in an area of roughly 3000 ha. on either side of the River Fafara between Zurmi and Dumburum, only 24 km. south of the international boundary.

Climate

The nearest station for which adequate meteorological data are available is Katsina, about 90 km. to the east of Zurmi and 13 minutes of latitude farther north. The recorded mean annual rainfall is about 710 mm. for a period of 23 years, but was slightly higher in the period 1925–35, to which the data in Table 1 refer.

Table 1

Month	Mean rainfall		Temperature (° C.)		Relative humidity	
	Amount in mm.	No. of days	Mean maximum	Mean minimum	Mean 9 a.m.	Mean 3 p.m.
January	0.3	0	30.0	13.0	22	18
February	Nil	0	32.7	15.2	20	16
March	0.5	0	38.0	19.0	25	15
April	6.3	1	40.2	22.5	33	17
May	61.2	6	38.1	23.5	56	32
June	90.7	7	35.2	21.1	68	48
July	151.4	12	31.7	20.6	79	68
August	281.2	17	30.0	20.9	86	72
September	129.0	11	31.4	21.3	81	65
October	9.6	1	34.0	20.0	58	30
November	0.3	0	35.0	16.9	26	16
December	Nil	0	31.0	13.8	28	14
Year	730.5	55	33.9	19.0	49	34

Isohyetal maps (see Fig. 2) show that the rainfall in the Zurmi area must be much the same as that of Katsina. The climate is typical of stations in the central part of the Sudan zone.

Geology and topography

The whole area is occupied by granites and gneisses of the ancient basement complex, which forms the central massif of northern Nigeria. It is probable that during an arid phase of the Quaternary a mantle of sand (mostly of local origin) was laid over the irregular surface of the crystalline rocks. This mantle of sand, sometimes very thick, sometimes quite thin, makes the present general land surface more or less level. The sandy mantle is frequently pierced by rock outcrops, either because it was insufficient to cover them or because of subsequent denudation. Some outcrops are merely surface exposures, while others are 'whale-back' hills, or heaps of boulders, up to 40 m. high. A hill called Dutsen Bagai, and two others near it, are composed of very hard black boulders of garnetiferous quartzite and a basic rock of the Charnockite group.

In the valley of the Fafara river (see Fig. 3) steep rocky slopes separate the sandy alluvium of the river terraces from the general high level ground of the surrounding

country. A number of small tributaries join the Fafara inside the Reserve. They are mostly quite short and are completely dry in the dry season; many of them commence in *Acacia seyal* semi-basin sites (see p. 356), and enter the main stream in steep-sided gulleys.

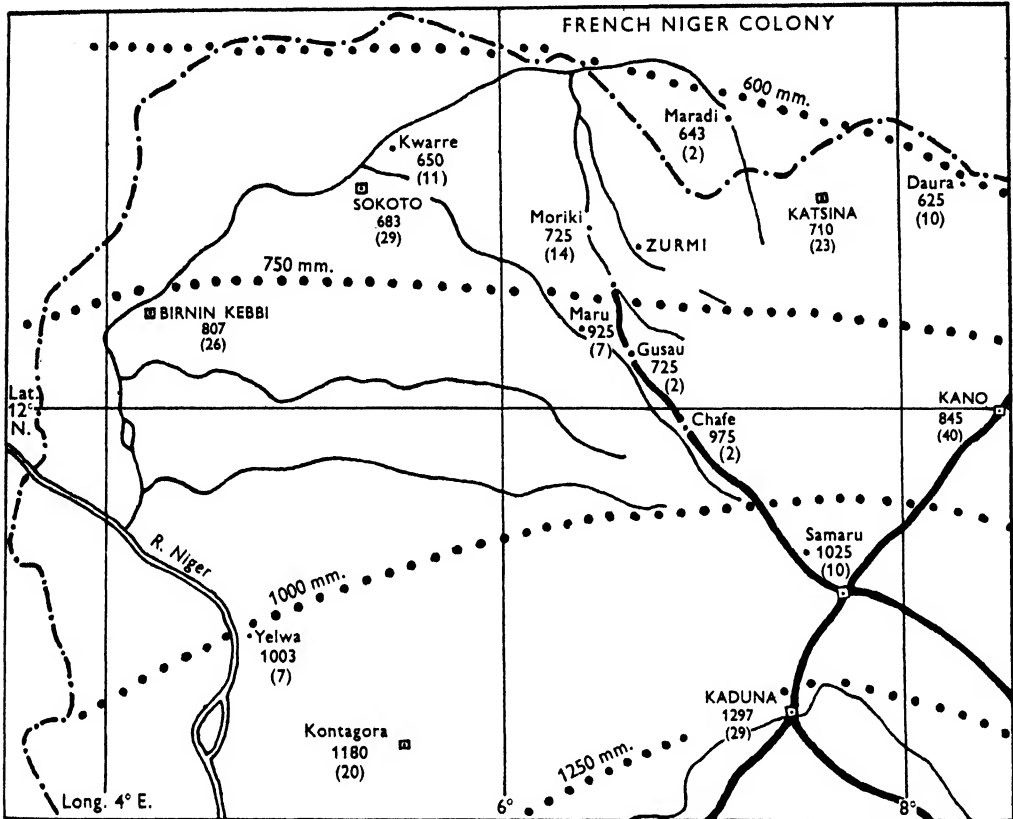


Fig. 2. Isohyetal map of north-western Nigeria. (Mean annual rainfall in mm. is shown beneath each station, the figure in brackets referring to the number of years on which the mean is based.)

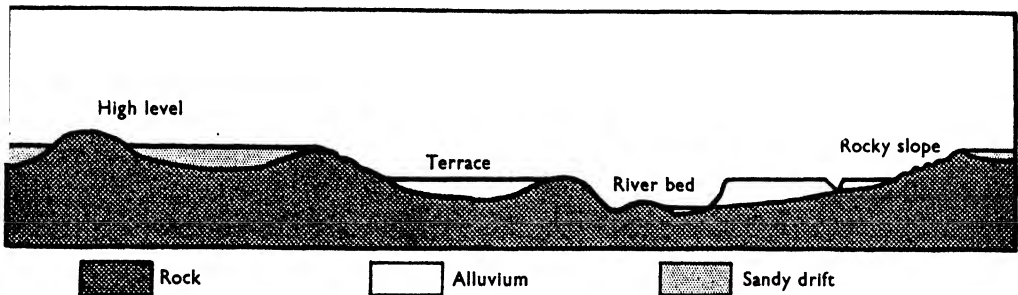


Fig. 3. Diagrammatic section of the Fafara valley.

History

Information has been obtained from the writings of Clapperton & Denham (1828), Barth (1857), Hogben (1930) and Niven (1937). Clapperton passed through Zurmi in May 1824, and it is clear from his account that the surrounding country was fully occupied and had been

so for a century or more. These were troublous times, however, owing to the Fulani rising which started at Sokoto in 1804. Barth, who visited Zurmi in 1853, noted that Zamfara 'is at present divided into petty states each of which follows a different policy'. Some towns adhered to the original rulers, while others supported the Fulani, but no matter what its allegiance any small town or village was liable to be ruthlessly raided by its enemies. Through this kind of fighting the country which is now Forest Reserve became uninhabited, the people either fleeing to the large towns, or else being slaughtered, or carried off as slaves, while their farmlands became covered with comparatively dense savanna vegetation.

As far as one can gather, raiding and punitive expeditions continued in Zamfara from Barth's time right up to 1902 when the British expedition arrived at Sokoto. During the peace which followed, the tendency in Sokoto, as elsewhere, has been for people to spread from the larger towns into the surrounding country which the Fulani wars had rendered desolate. It appears, however, that the area which is now the Zamfara Forest Reserve has remained more or less uninhabited since Barth's time. In fact, the Reserve was constituted in 1919 because most of the area was uninhabited.

Biotic influences

(1) *Farming*

It is evident that much of the vegetation has grown up on abandoned farms and villages during the past 80 or 90 years. The descriptions of Clapperton and Barth show that this farmland must have looked much the same as that of Zurmi to-day.

The Zurmi farmlands are of three main types:

(a) Dry sandy soils of high-level sites are cultivated for millet, guinea corn and ground-nuts. Excellent crops are grown each year, fertility being maintained by sweepings and manure brought out of the town, and by the droppings of cattle, sheep and goats which feed on stubble left after harvest. Very few trees are kept on these farms and the ground is cleared almost completely of woody roots.

(b) Sandy terraces (up to 200 m. wide) of alluvial land on either side of the River Fafara are intensively farmed: tobacco, cotton, guinea corn, cassava and onions being grown. Zamfara has been famed for its onions for many years; thus Barth (1857) of 1853 writes: 'Neither was there any scarcity of onions, a vegetable which is extensively cultivated in the province of Zamfara.' The onion farms are watered in the dry season by a *shadoof*. Large trees are preserved in these farms and on the river banks themselves. Tangles of scandent shrubs remain in rocky places and in the gorges of tributary streams.

(c) Beyond the permanent farmlands which surround a Hausa town there is a zone cultivated on a rotation of 5 or more years with 'bush fallow'. Woody stumps and roots are left in the ground, and regrowth of savanna is quickly established when the farm is abandoned. Occasional large trees are left on the farm, and the regrowth vegetation has, in consequence, a characteristic two-storeyed structure. In this district cattle are grazed on the fallow land and they appear to be responsible for the abundance of *Piliostigma reticulatum* (to 5 m. high), whose pods they eat.

Rocky slopes and hills are not cultivated but are usually cut over for firewood, and may be used for rough grazing, especially by goats. In the cutting of fuel and poles it is usual for the small trees and coppice to be cut in preference to the larger trees. This tends to produce an irregular 'coppice-with-standards' structure in the savanna.

Between the years 1850 and 1919 there was probably some spasmodic farming in what is now the Forest Reserve, especially on the fertile river terraces. Since 1919 there has probably been none.

(2) *Grass fires*

Before reservation grass fires were probably annual though their intensity must have varied from place to place and from year to year. Since reservation a system of 'early burning' has been introduced, whereby the grass is burnt at the beginning of the dry season as soon as it is dry enough to burn. In this way the fierce burning of tinder-dry savanna late in the dry season is avoided.

Grass is seldom more than 1.5 m. high, and in many places it is sparse and barely 1 m. high. The fires cannot, therefore, be as fierce and devastating as in the wetter Guinea zone, where grass is dense and anything from 1.5 to 4 m. high.

(3) *Cattle*

Hausaland has always been noted for the large herds of cattle, owned by the nomadic Fulani, which graze in the savannas and farms. During the unsettled times of the last century they probably avoided the country east of Zurmi, but are common there to-day.

A year before my visit some Fulani had illegally camped in the Reserve and stayed there for 3 days. A circle about 120 m. diameter had been cleared of all but the largest trees, and the wood used for fires and for making rough beds and shelters. Such clearances are unusual in a fairly well-patrolled reserve, but before 1919 they were probably more widespread and their effect on the vegetation must be borne in mind. A striking remnant of the camp was a group of fruiting calabash plants (*Lagenaria vulgaris*); probably a Fulani wife had cleaned a calabash during her short stay and left the seeds on the ground!

Cattle seem to have influenced the vegetation in several different ways. They graze and trample down grass, other herbs and the seedlings and suckers of woody species. This is particularly noticeable along recognized trade routes where the cattle may affect a belt up to 200 m. or so wide. The effect of this trampling is twofold. On the one hand, grass fires are practically eliminated, completely so in the heavily trampled areas; while on the other hand, young coppice sucker and seedlings shoots tend to be destroyed. The effect this has on the regeneration of *Anogeissus leiocarpa* is very striking (see p. 347). African paths change direction from time to time and there are many small areas which were apparently heavily trampled but have subsequently been left more or less untouched.

Field methods

The field work was done in 3 weeks during April and May 1946, and formed part of a practical course of instruction for students of the Ibadan Forest School.

Four transect lines were marked on the ground and levelled with an Abney Level. Lines 1, 2 and 3 were 3.2 km. long and started on the banks of the Fafara, but Line 4 was 1.6 km. long and ran between two hills.

Thirty-six 0.4 ha. (1 acre) plots were sited on, or near, the transect lines in what appeared to be more or less distinct communities. These plots were enumerated by students, data for some of the plots being given in this paper. Plots of this size (40 by 100 m.) were found to be convenient. In vegetation, which is an intricate mosaic of different communities,

a large plot is undesirable; even with 0.4 ha. care was needed to ensure that only one type of woodland community was sampled by each plot.

Forty-five soil pits were dug along the four lines to sample, as far as possible, the main soil types. Profile descriptions and diagrams were made for each pit. The enumeration plots and soil pits are numbered according to their position on the transect lines; thus Pit 2/381 is 381 m. from the start of Line 2.

Profile diagrams of the vegetation were drawn at various places along the transect lines, a total distance of nearly 1.5 km. being covered in this way. The strips were 6.1 m. (20 ft.) wide; tree heights were estimated by eye. Some of the diagrams are reproduced in Figs. 5 and 6.

Altogether 240 botanical specimens were collected. A complete set has been deposited in the Forest Herbarium at Ibadan and duplicates of many numbers have been distributed to Kew, the British Museum and the Imperial Forestry Institute, Oxford. A list of woody species is given in the appendix. Owing to the season of the year it was impossible to study the herb layer.

III. VEGETATION FORM

General

Many plant communities are recognized generally by their distinctive physiognomy and habitat, and in Britain are given simple everyday names, such as hedgerow, carr, parkland and heath. The physiognomy and general habitat of the community is recognized, irrespective of ecological status, size or floristic composition. Simple terms, such as those mentioned above, describe what may conveniently be called the *form* of the community. They do not necessarily fit easily into a classification based on succession, particularly where the vegetation is an artificial or deflected seral type. The ecologist, as well as the forester, does, however, frequently need to describe the *form* of artificial communities, or of communities whose successional status is not at once apparent, and does in fact often use a simple word descriptive of *form* rather than a more cumbersome technical definition.

In the tropics ecologists and foresters have had to invent their own terms for describing vegetation; some have used local vernacular names while others have tried to name communities according to their successional status. This has inevitably led to confusion, particularly when the successional status has been wrongly assessed. There is a long-felt need for some degree of standardization, at least of terms descriptive of *form*.

In Nigeria an attempt has been made to standardize in a small handbook of the Forest Department (1948) terms descriptive of *form*. The terms used in the present paper are those of this handbook, except for *open savanna woodland* which is used here for a common type in which the trees are fairly closely and evenly spaced but do not form a closed canopy. The word *savanna* (as opposed to *forest*) is used generally for communities in which tall bunch-grasses are dominant in the herb stratum, no matter whether the trees are widely or closely spaced. In *savanna woodland* the trees form a more or less complete canopy, while in *open savanna* the trees are widely separated.

Stratification

It is convenient to distinguish four more or less distinct strata in the savanna vegetation of West Africa; in Zamfara these are:

Upper Tree Stratum	Shrub Stratum
Lower Tree Stratum	Herb Stratum

The *Upper tree stratum* consists of relatively tall trees, over about 6 m. and often 12–15 m. high, usually with spreading crowns. Of these *Anogeissus leiocarpa* is by far the commonest; the bole of this species is usually short and the crown is spreading, but most other trees have relatively tall straight boles. Other species which occur commonly in this stratum are *Balanites aegyptiaca*, *Lannea microcarpa*, *Sclerocarya birrea*, *Sterculia setigera*, *Prosopis africana* and *Boswellia dalzielii*. Of less common occurrence are *Butyrospermum parkii*, *Tamarindus indica*, *Albizzia chevalieri*, *Lonchocarpus laxiflorus*, *Diospyros mespiliformis*, *Ficus platyphylla* and the palm *Hyphaene thebaica*. Several of the smaller trees occasionally reach this stratum.

The *Lower tree stratum* consists of trees up to about 6 m. high. *Strychnos spinosa* and *Combretum glutinosum* are by far the commonest, though *Terminalia avicennioides* is locally abundant. Other species which occur less frequently are *Piliostigma reticulatum*, *Acacia seyal*, *A. senegal* and *Annona senegalensis*. Young trees of the upper stratum are also represented and may be abundant in regrowth stages.

In some forms both upper and lower strata are equally represented, but in others one or other assumes dominance.

The *Shrub stratum* includes both erect and scandent shrubs, as well as coppice, sucker and seedling regrowth of trees. The commonest erect shrubs are *Gardenia erubescens*, *Ximenia americana*, *Fluggea virosa*, *Guiera senegalensis*, and *Randia nilotica* which often reaches 4 or 5 m. high. *Combretum micranthum* frequently occurs as a low shrub, but its optimum growth is as a large scandent shrub or liane. *Capparis corymbosa* is another scandent shrub, but it is often found as a rounded bush neatly cropped by cattle. The shrub stratum is never continuous, except on rocky hills and by water-courses.

The *Herb stratum* is dominated by perennial grasses, up to about 1.5 m. high. Unfortunately, the present work was done near the end of the dry season when the ground was almost everywhere burnt bare. Occasional perennials such as *Evolvulus alsinoides* and *Pergularia tomentosa* were just forming fresh shoots and flowers, but it was impossible to study the herbaceous communities.

Leaf size

A feature of Sudan zone vegetation, which is noticed by the traveller from the Guinea zone, is the increase in the proportion of fine-leaved and thorny trees. The general impression is that broad-leaved trees are dominant in the Guinea zone, whereas in the Sahel zone fine-leaved thorny species dominate, so much so that the vegetation has often been called Thornland. In the Sudan zone, however, fine and broad-leaved trees and thorny species seem to be mixed. As a check on the accuracy of this general impression an analysis of the Zurmi flora was made with regard to Raunkier's leaf sizes. For this purpose the ninety-two woody species listed in the Appendix (p. 363) were classified into the standard leaf (or leaflet) sizes with the following results:

Leptophyll	12	Macrophyll	1
Nanophyll	8	Megaphyll	Nil
Microphyll	36	(Palm trees	2)
Mesophyll	33		

This shows a more or less equal proportion of microphylls and mesophylls, with the twelve leptophylls and eight nanophylls giving a definitely fine-leaved appearance. Eight of the twelve leptophylls are species of *Acacia*, and three others are Mimosaceae. The only

macrophyll is *Ficus platyphylla*. Of the ninety-two woody species, twenty-two have thorns—that is 24%.

IV. PLANT COMMUNITIES IN RELATION TO SOIL AND BIOTIC INFLUENCES

The importance of micro-relief in determining the catenary and mosaic arrangement of soil types and plant communities in African savanna has been emphasized by Morison *et al.* (1948). In the Zurmi area, however, this basic arrangement is somewhat obscured by overriding biotic influences. These influences are not uniform either in kind or in time, and only small isolated areas may be affected by the same set of factors at the same time. There is, therefore, an extremely complicated mosaic of numerous secondary seral communities at various stages of development and influenced by various biotic factors or combinations of factors, superimposed on the soil catenas and mosaics.

The vegetation of the Aweil transect described by Morison *et al.* (1948) corresponds closely to parts of the Sudan zone in West Africa. The Aweil catena-variant is in country of low relief and very gentle slopes, little above the level of large rivers; the low level, or *illuvial*, complex therefore comprises most of the regional ecosystem. The Zurmi area, although comparable to Aweil floristically, is however very different topographically, the bulk of the land being *high level*, well above the flood level of the rivers which flow through relatively steep rocky valleys. The low level complex is, therefore, poorly developed.

In addition to the main catenas orientated in relation to the main river (at Zurmi the Fafara), each tributary stream has its own catena. This means that low-level sites of a tributary catena are often higher than parts of the main catena. In the interpretation of a soil-vegetation unit it is therefore important to decide whether it is part of the main or the tributary catena.

The main parts of the catenas in the Zurmi area are:

- A. High level—covering most of the area.
- B. Rocky hills and slopes—mosaics of colluvial and eroded soils.
- C. Low level—including low level portions of the tributary catenas as well as those of the main catena.

Rather unusual soils and vegetation were found on the sites of deserted villages; these are described separately.

High-level sites

(1) *Soil*

A certain amount of geological evidence, which cannot be considered here, suggests that arid and pluvial phases alternated during the Quaternary age in West Africa. The prevalence in the past of desert-like conditions in the Zamfara area evidently explains certain features of the soils as they are to-day. Soil pits show that a varying depth of superficial wind-blown sand covers the *in situ* weathering rock. In places a layer (up to 1 m. thick) of coarse quartz and felspathic material with a little clay (called here the clay-rubble layer) separates the superficial sand from the weathering rock.

The parent rock contains a high proportion of quartz, and so it may safely be assumed that the *in situ* soils built up before the arid phase were very sandy. With the advent of desert or semi-desert conditions such a sandy soil would naturally dry out and be blown about by the wind. In this way the surface of the land would be levelled off by a mantle of wind-blown sand. Sand moving southwards from desert country would assist in this

process, but the absence of old dunes suggests that there was no major movement of sand, and that most of the mantle is of local origin.

The parent material available for soil formation in the moister period which followed consisted, therefore, of the irregular surface of the basement rocks, probably quite fresh, covered by a varying thickness of wind-blown sand, sometimes with an intermediate clay-rubble layer. Beneath this mantle the parent rock would start to weather again by chemical processes as opposed to the physical weathering which would have been dominant in the arid phase. The weathering material retains the general appearance and banded structure of the solid rock. Particles of weathering biotite and feldspar can be identified, but the rock is rich in quartz and the weathered material is mostly sandy.

A feature of the soils in this area is the abundance of unweathered or partly weathered particles of feldspar which occur in the clay-rubble layer, and also to a lesser extent in the superficial sand. It is possible that even to-day conditions are too dry for rapid weathering of feldspars.

The clay-rubble layer probably represents the coarse fraction which was left when smaller sand particles were blown about. The fact that it is sometimes absent altogether indicates that it is not an essential stage in present soil-forming processes. The layer shows no sign of the structure of the underlying rock and contains no veins of quartz or quartzofeldspathic pegmatite, such as commonly extend from the rock into *in situ* soils.

Based upon the varying depths of the superficial sand and the presence or absence of the clay-rubble layer, the soils of the high-level complex may be classified as follows:

TYPE A. Sand over clay-rubble with weathering rock 1.5–2 m. from the surface. Fig. 4 shows the profile of a typical pit (No. 2/381), which was described as follows:

0–82 cm. Pale brown fine sand, loose, dry, with occasional particles of feldspar. Merging.
82–153 cm. Pale brown fine and coarse sand with clay, pieces of angular quartz, feldspar and weathering granite, conspicuous manganese concretions; hard, now dry. Well defined.
153–165 cm. (bottom of pit). Weathering granite.

Although dry in May at the end of the dry season, the clay-rubble layer (82–153 cm.) appears to retain a certain amount of moisture, thus making soils of this type relatively favourable.

TYPE B. Sand directly over rock. Fig. 4 shows the profile of a typical pit (No. 1/549), which was described as follows:

0–119 cm. Pale brown structureless sand; pieces of gneiss to 45 cm. in diameter found near bottom with brown weathered outer crust. Well defined.
Bottom of pit. Hard, but weathering, gneiss.

It seems clear that this type of profile has been formed by wind-blown sand, covering up a more or less fresh surface of *in situ* rock which has since begun to weather. The type varies according to the depth of the rock.

TYPE C. Deep sands. In several pits neither the clay-rubble layer nor the weathering rock was reached. Profiles of this nature, in which the clay-rubble layer may or may not be present, are grouped together as Type C. Fig. 4 shows the profile of a typical pit (No. 2/2379), which was described as follows:

0–51 cm. Grey-brown fine structureless sand with small pieces of feldspar, loose, dry; darker above, pale below. Merging gradually.
51–127 cm. (bottom of pit). Pale brown (slightly reddish), fine sand with rotting feldspar; dry, hard; no sign of rock.

These soil types alternate frequently in the high-level mosaic, and their distribution does not appear to be related to any obvious features of surface relief.

Correlation between vegetation and soils in this mosaic is not immediately obvious, partly because of biotic interference and partly because the soil variations cannot be seen without pits. As far as the vegetation is concerned, the important variation in the soil appears to be the presence or absence of the clay-rubble layer with its water-retaining properties.

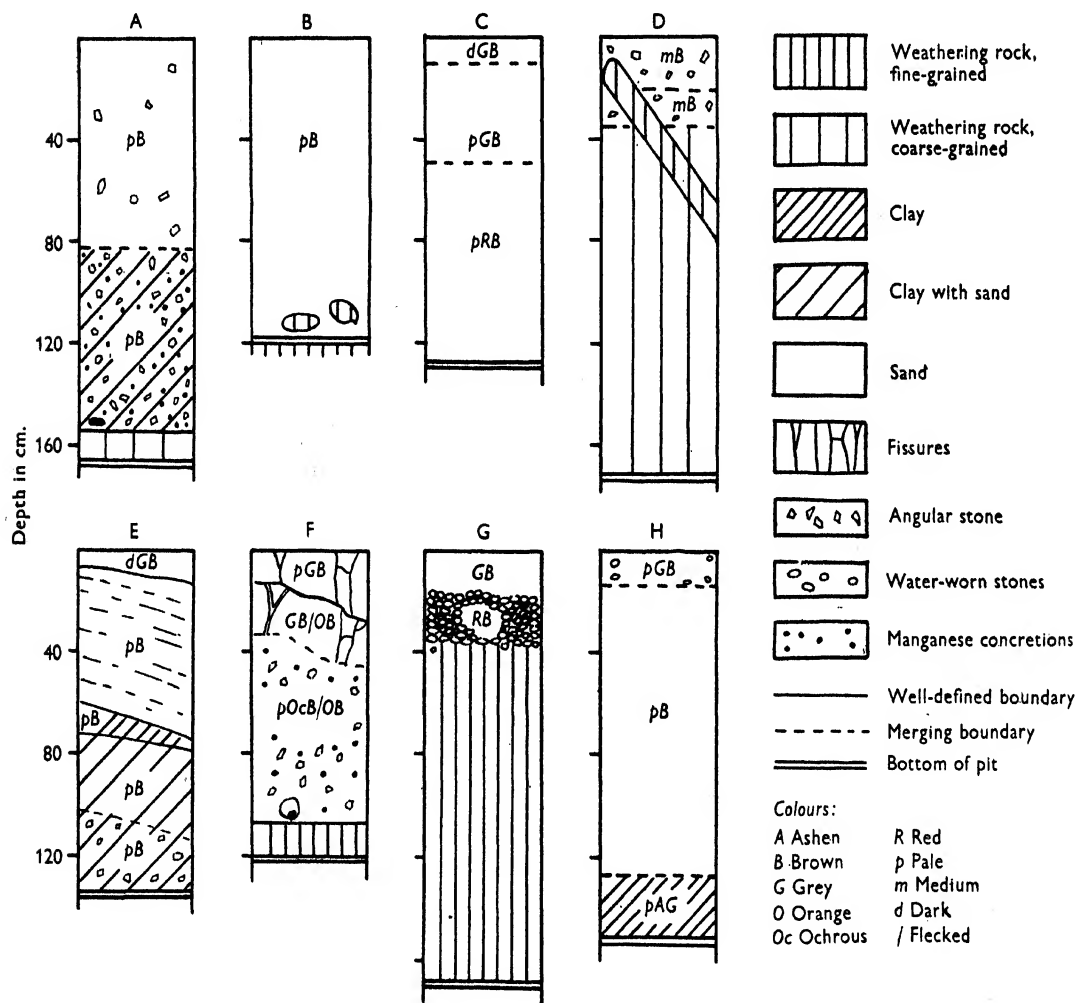


Fig. 4. Soil profiles of pits typical of the main soil types (A to H).

(2) Vegetation

The three most abundant trees on high-level sites are *Anogeissus leiocarpa*, *Combretum glutinosum* and *Strychnos spinosa*. *Combretum* and *Strychnos* appear to have similar ecological requirements and together, or separately, they are dominant in communities which avoid the moister soils with the water-retentive clay-rubble layer (Type A) and tolerate the drier sands (Types B and C). *Anogeissus*, on the other hand, tends to be dominant on Type A soils.

The three species may be mixed, but more usually one or other is dominant. Where

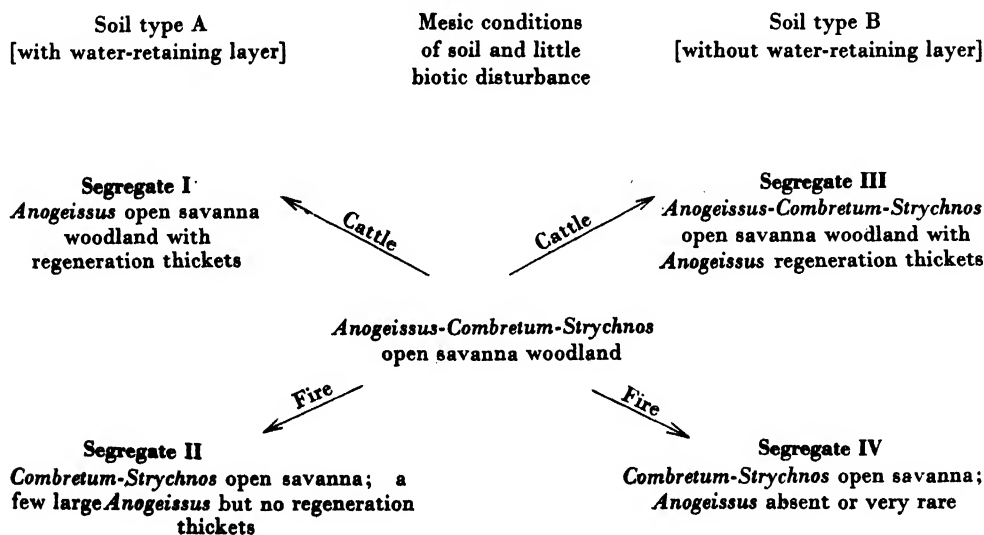
Anogeissus is abundant *Combretum* and *Strychnos* are either absent or rare, and where the other two species are dominant *Anogeissus* is rare. In four enumeration plots (0.4 ha.) more than 70% of the trees are *Anogeissus*; in three of these four plots *Combretum* and *Strychnos* are absent, and in the fourth they make up only 4%. *Combretum glutinosum* and *Strychnos spinosa* make up over 55% of the trees in five plots, none of which has more than 8% *Anogeissus*.

The mosaic of communities dominated either by *Anogeissus* or by *Combretum-Strychnos* corresponds to some extent to the mosaic of soil types, but the vegetation mosaic is complicated by biotic interference.

Most of the vegetation has grown up on cultivated lands, but cultivation is no longer an active determining factor. To-day the important factors are grass fires and cattle. The fire tends to keep the vegetation open, to eliminate certain species, and hence selectively to favour fire-resistant species, especially *Combretum glutinosum* and *Strychnos spinosa*. The effect of cattle is more complex and may work in opposition to the fire factor. Trampling and grazing reduce the grass cover, especially by main cattle routes, and thereby stop grass fires not only on the trampled area but also in untrampled patches surrounded by trampled 'fire-breaks'. This fire protection favours the regeneration of trees, especially of *Anogeissus*, whose early stages are very sensitive to fire; old trees of *Anogeissus* are, however, fairly resistant. The foliage of *Anogeissus* is distasteful to cattle; thus once a thicket of young growth is established it is avoided by the animals.

The abundance of *Anogeissus* by cattle routes is most striking. All stages from young thickets to mature woodland are present. In the early stages *Anogeissus* is mixed with *Dichrostachys glomerata*, but the latter is seral and does not persist.

The complex action of the soil mosaic and the two main biotic factors upon the vegetation is best understood by considering an 'ideal' mesic community in which *Anogeissus* (upper stratum) and *Combretum* and *Strychnos* (lower stratum) are codominant trees. Such a community exists under what appear to be mesic conditions of soil and relatively little biotic disturbance. Under the influence of more extreme edaphic or biotic factors the three dominants segregate, as indicated in the following diagram.



This segregation of the dominant species, under the influence of edaphic and biotic factors, appears to be comparable to the *association-segregation* of the forests of North America described by Braun (1935). The Zamfara communities are certainly not climax and so the term *associes-segregate* is used here.

Segregates I and IV are the most distinct because the two sets of factors work in the same direction. In Segregates II and III the factors work in different directions, and the resulting communities are of an intermediate type. The biotic factors do not necessarily remain constant either in kind or intensity, and the vegetation mosaic may be further complicated by the initiation of, say, cattle trampling in Segregate II, or of fire in Segregate III, when these would tend to change to Segregates I and IV respectively.

The foregoing explanation is based only on observations of the vegetation as it is to-day, the effect of the biotic factors not having been tested in controlled experiments. The biotic factors at present controlling any particular community and the ecological behaviour of the more abundant species are, however, evident in this vegetation which may be regarded as a mosaic of numerous natural experiments. The hypothesis of *associes-segregates* does, at all events, go a long way in explaining the mosaic which at first sight seems unordered. Six communities (sampled by 0.4 ha. plots) are described below as examples of: (a) a community approximating to the mesic type, (b)–(e) the four main *associes-segregates*, and (f) a community which is evidently transitional between Segregates III and IV.

(a) *Mesic type*: *Anogeissus-Strychnos-Combretum*, open savanna woodland.

Position: Line 1/2199–2299; area of plot 0.4 ha.

Soil: Type A.

Vegetation form: open savanna woodland.

Floristic composition: *Anogeissus leiocarpa* dominant in the upper stratum, *Strychnos spinosa* and *Combretum glutinosum* dominant in the lower stratum *Guiera senegalensis* (l.f.) as low shrub.

Enumeration of trees:*

Species	Girths in cm.										Total
	5–15	15–30	30–45	45–60	60–75	75–90	90–105	105–120	120–135	135–150	
<i>Anogeissus leiocarpa</i>	8	15	14	7	3	5	52
<i>Sclerocarya birrea</i>	.	.	4	.	.	1	.	.	2	2	9
<i>Prosopis africana</i>	.	.	2	1	.	3
<i>Balanites aegyptiaca</i>	.	.	.	1	.	.	1	.	.	.	2
<i>Lannea microcarpa</i>	1	.	.	.	1
<i>Strychnos spinosa</i>	18	17	3	1	2	41
<i>Combretum glutinosum</i>	8	8	3	.	1	20
<i>Acacia seyal</i>	.	.	.	1	1
<i>Acacia senegal</i>	1	1
<i>Annona senegalensis</i>	.	.	.	1	1
<i>Combretum nigricans</i>	1	1
<i>Diospyros mespiliformis</i>	1	1
Total	37	40	26	11	6	6	2	.	3	2	133
Number of trees per hectare:				192 under 30 cm. girth							
				140 over 30 cm. girth							
				332 total							

Regrowth shoots of tree species: *Strychnos spinosa* (f.), *Combretum glutinosum* (f.), *Anogeissus leiocarpa* (r.).

Although still mesic in composition this community is evidently tending towards Segregate II under the

* In these enumerations the girths of all trees were measured at about 1.3 m. from the ground. The results have been set out to show in order of abundance: first, the species composing the upper stratum, and secondly those composing the lower stratum. 'Regrowth shoots of trees species' includes seedlings and coppice and sucker shoots below 5 cm. girth.

influence of grass fires. Regrowth shoots of *Strychnos*, and *Combretum* are frequent, but *Anogeissus* is apparently not regenerating owing to fire.

(b) *Segregate I*: *Anogeissus*, open savanna woodland with regeneration thickets.

Position: Line 3/976-1076, within the limits of the main Zurmi-Dumburum cattle track; area 0.4 ha.

Profile No. 6 (Fig. 6).

Soil: Type A.

Vegetation form: open savanna woodland, with regeneration thickets; widely spaced large trees (12-15 m. high), scandent shrubs occasional.

Floristic composition: larger trees almost all *A. leiocarpa*; regeneration thickets *Anogeissus* and *Dichrostachys glomerata*; scandent shrubs *Combretum micranthum* and *Acacia ataxacantha*; *Capparis corymbosa* as browsed bush.

Enumeration of trees:

Species	Girths in cm.								Total
	5-15	15-30	30-45	45-60	60-75	75-90	90-105	105-120	
<i>Anogeissus leiocarpa</i>	74	90	14	1	1	.	.	1	181
<i>Lanea microcarpa</i>	1	1	1	1	1	.	.	.	5
<i>Sclerocarya birrea</i>	.	1	1	.	1	.	.	.	3
<i>Balanites aegyptiaca</i>	1	.	.	.	1
<i>Albizzia chevalieri</i>	.	1	1
<i>Acacia seyal</i>	1	1	.	.	1	.	.	.	3
<i>Commiphora pedunculata</i>	3	1	4
<i>Ximenia americana</i>	.	.	1	1
<i>Combretum nigricans</i>	.	1	1
Total	79	96	17	2	5	.	.	1	200

Number of trees per hectare: 438 under 30 cm. girth
62 over 30 cm. girth
500 total

Regrowth shoots of tree species: *Anogeissus leiocarpa* (v.a.) and *Dichrostachys glomerata* (v.a.); the latter is also abundant as a small tree but was omitted from the enumerations.

The dominance of *Anogeissus* is complete in this consociation on which both edaphic (Type A soil) and biotic (cattle trampling) factors work in the same direction.

(c) *Segregate II*: *Combretum-Strychnos*, open savanna.

Position: Line 2/1359-1459; area 0.4 ha.

Soil: Type A.

Vegetation form: open savanna, trees widely spaced and mostly of the lower stratum; erect shrubs frequent.

Floristic composition: *C. glutinosum* and *Strychnos spinosa* codominant, *Anogeissus leiocarpa* rare; *Gardenia erubescens* (a.) and *Randia nilotica* (f.) as erect shrubs.

Enumeration of trees:

Species	Girths in cm.								Total
	5-15	15-30	30-45	45-60	60-75	75-90	90-105	Over 105	
<i>Prosopis africana</i>	.	3	.	1	2	1	.	.	7
<i>Anogeissus leiocarpa</i>	1	.	.	1	1	.	.	1-150/165	4
<i>Strychnos spinosa</i>	5	8	3	1	17
<i>Combretum glutinosum</i>	6	8	1	.	1	.	.	.	16
<i>Annona senegalensis</i>	1	.	6	1	.	1	.	.	9
<i>Terminalia avicennioides</i>	2	1	1	.	1	.	1	.	6
<i>Piliostigma reticulatum</i>	.	1	.	1	.	.	1	.	3
<i>Lanea microcarpa</i>	1	1
<i>Gymnosporia senegalensis</i>	.	.	1	1
<i>Butyrospermum parkii</i>	.	.	1	1
Total	16	21	13	5	5	2	2	1	65

Number of trees per hectare: 93 under 30 cm. girth
70 over 30 cm. girth
163 total

Regrowth shoots of tree species: *Combretum glutinosum* (f.); *Piliostigma reticulatum* (o.), *Terminalia avicennioides* (o.).

The important effect of fire in this associates-segregate is seen in the relative abundance of *Combretum* and *Strychnos* on a soil (Type A) which normally favours *Anogeissus*, and in the very open structure of the low scrubby savanna.

Throughout most of the Zurmi area *Terminalia avicennioides* is rather uncommon, but locally it is dominant in small communities (see Profile No. 4 in Fig. 6). The *Terminalia* consociates appears to be a variant of Segregate II, occurring on soils of Type A and in areas where grass fires rather than cattle appear to be the dominant biotic factor. It may be, however, that past conditions of cultivation are also important in determining the abundance of *Terminalia*.

(d) *Segregate III: Anogeissus-Sclerocarya-Strychnos, open savanna with Anogeissus regeneration thickets.*

Position: Line 1/300-400; area 0.4 ha.

Soil: Type B.

Vegetation form: open savanna, with widely spaced upper stratum trees, and thickets of young trees.

Floristic composition: *A. leiocarpa* and *Sclerocarya birrea* dominant, both as large trees and as young trees in thickets; *Strychnos spinosa* and *Combretum glutinosum* are the commonest of the lower stratum trees; *Ximenia americana* is frequent as a shrub.

Enumeration of trees:

Species	Girth in cm.									Total
	5-15	15-30	30-45	45-60	60-75	75-90	90-120	105-135	120-135	
<i>Anogeissus leiocarpa</i>	7	11	3	3	.	1	2	1	1	29
<i>Sclerocarya birrea</i>	13	4	.	1	.	.	1	.	1	20
<i>Lannea microcarpa</i>	1	.	.	.	1	1	.	1	.	4
<i>Albizzia chevalieri</i>	1	.	.	.	1
<i>Balanites aegyptiaca</i>	.	.	.	1	1
<i>Strychnos spinosa</i>	6	5	3	1	15
<i>Combretum glutinosum</i>	7	1	3	11
<i>Acacia seyal</i>	2	3	3	8
<i>Piliostigma reticulatum</i>	3	2	1	1	7
<i>Commiphora pedunculata</i>	3	.	2	1	6
<i>Ziziphus mauritiana</i>	.	.	1	1
Total	42	26	16	8	1	3	3	2	2	103

Number of trees per hectare: 170 under 30 cm. girth
87 over 30 cm. girth
257 total

Regrowth shoots of tree species: *Anogeissus leiocarpa* (f.) and *Sclerocarya birrea* (f.).

The soil here is that of the *Combretum-Strychnos* associates, but *Anogeissus* is in fact the most abundant tree and is regenerating in thickets; this is evidently due to the effect of cattle. The abundance of *Sclerocarya* is interesting; this species appears to flourish on the drier (Type B) soils, and to be favoured by fire-protection and cattle. *Sclerocarya* is absent from the plot described under Segregate II where both fire and the Type A soil oppose it, and is rare in Segregates I and IV. In the plot described as an example of the mesic type *Sclerocarya* is the next most abundant upper stratum tree after *Anogeissus*.

(e) *Segregate IV: Strychnos-Combretum, open savanna.*

Position: Line 1/498-598; area 0.4 ha.

Soil: Type B.

Vegetation form: open savanna, with well-developed lower stratum and only a few isolated larger trees.

Floristic composition: *Strychnos spinosa* and *Combretum glutinosum* codominant; *Randia nilotica* (f.), *Guiera senegalensis* (l.f.) and *Ximenia americana* (o.) are the commonest shrubs.

Enumeration of trees:

Species	Girth in cm.									Total
	5-15	15-30	30-45	45-60	60-75	75-90	90-105	105-120	Over 120	
	15	30	45	60	75	90	105	120	1—150/165	
<i>Lannea microcarpa</i>	.	.	.	3	.	1	.	2	.	7
<i>Sclerocarya birrea</i>	2	.	.	.	1	.	1	.	.	4
<i>Prosopis africana</i>	1	1	.	2
<i>Anogeissus leiocarpa</i>	.	1	.	.	.	1	.	.	.	2
<i>Albizzia chevalieri</i>	1	.	.	.	1
<i>Lannea schimperi</i>	1	.	.	.	1
<i>Stereospermum kunthianum</i>	1	.	.	.	1
<i>Strychnos spinosa</i>	27	16	7	1	51
<i>Combretum glutinosum</i>	21	13	2	8	2	1	.	.	.	47
<i>Piliostigma reticulatum</i>	1	4	5	1	1	12
<i>Commiphora pedunculata</i>	2	7	1	.	.	1	.	.	.	11
<i>Combretum nigricans</i>	4	2	.	1	.	1	.	.	.	8
<i>Annona senegalensis</i>	.	1	1	2
<i>Balanites aegyptiaca</i>	.	1	.	1	2
<i>Entada sudanica</i>	1	1	2
<i>Ziziphus mauritiana</i>	.	1	1
<i>Commiphora africana</i>	.	1	1
Total	58	48	16	15	4	8	2	3	1	155

Number of trees per hectare: 265 under 30 cm. girth

122 over 30 cm. girth

387 total

Regrowth shoots of tree species: *Combretum glutinosum* (a.), *Strychnos spinosa* (f.), *Combretum nigricans* (f.).

This is a well-marked community with both the soil (Type B) and the grass fires selectively favouring the tolerant species.

An interesting variant of this associates-segregate occurs in which *Prosopis africana* is rather more frequent than *Combretum glutinosum* and *Strychnos*. In thirty-two out of the thirty-six enumeration plots *Prosopis* is absent or represents less than 5% of the total trees. In the remaining four plots the proportions are 13% in two plots, 19 and 22%, and in all these plots the soil is of Type B (or C) and *Combretum glutinosum* and *Strychnos* are the codominant trees. It seems that *Prosopis* is a natural member of Segregate IV but that its present local distribution is due to felling. It is a favourite wood for charcoal and other domestic purposes, and even in the Forest Reserve a group of *Prosopis* was seen in which all the trees had been ring-barked in preparation to felling.

(f) *Segregate III, transitional to Segregate IV: Anogeissus-Combretum-Strychnos, open savanna with relict Anogeissus and invading Combretum*

Position: Line 1/720-820; area 0.4 ha.

Soil: Type C (deep sand).

Vegetation form: open savanna with both upper and lower strata represented but both open; erect shrubs frequent.

Floristic composition: *Anogeissus leiocarpa* dominant in the upper stratum, but without regeneration; *Combretum glutinosum* and *Strychnos spinosa* dominant in the lower stratum, the former with abundant regrowth; as erect shrubs are *Fluggea virosa* (f.), *Guiera senegalensis* (l.f.) and *Ximenia americana* (o.); *Capparis corymbosa* (o.) is a scandent shrub.

Enumeration of trees:

Species	Girth in cm.										Total
	5-15	15-30	30-45	45-60	60-75	75-90	90-105	105-120	120-135	135-150	
<i>Anogeissus leiocarpa</i>	6	.	3	.	1	.	2	1	1	1	16
<i>Balanites aegyptiaca</i>	2	.	2	.	.	1	.	2	.	.	8
<i>Entada sudanica</i>	1	2	1	.	.	.	4
<i>Piliostigma reticulatum</i>	1	.	.	2	.	.	3
<i>Lannea microcarpa</i>	2	2
<i>Sclerocarya birrea</i>	1	1	2
<i>Adansonia digitata</i>	1	1
<i>Combretum glutinosum</i>	14	4	1	19
<i>Strychnos spinosa</i>	11	7	.	1	19
<i>Combretum nigricans</i>	5	2	7
<i>Ziziphus mauritiana</i>	3	3
<i>Commiphora pedunculata</i>	.	1	1	2
<i>Acacia seyal</i>	.	.	1	1
Total	42	14	8	1	3	6	3	5	1	2	87

Number of trees per hectare: 140 under 30 cm. girth
77 over 30 cm. girth

217 total

Regrowth shoots of tree species: *Combretum glutinosum* (a.), *Balanites aegyptiaca* (o.).

The suggestion here is that cattle have previously caused the abundance of *Anogeissus* which is still dominant in the upper stratum, but that its regeneration has been curtailed by the entry of fire. *Combretum glutinosum* is now invading and a change from Segregate III to IV is taking place.

Rocky hills and slopes

(1) Soils

Any slope of more than about 2° gradient is liable to severe erosion in this area. The superficial layer of sand is easily removed as well as the sandy material derived from the *in situ* rock. Under the prevailing conditions it appears that much of the eroded material is carried direct to low-level sites and that zones of colluvial material are limited. On rocky slopes the outcrops and boulders may hold up pockets of colluvial soil and possibly moisture too. The rocky slope consists therefore of a mosaic of eroded and colluvial soils amongst bare outcrops and boulders. Most of the slopes in this area are rocky so this mosaic is often met with.

The characteristics of the eroded and colluvial soils are most clearly seen on a slope free from rocks. On such a slope the eroded soil is found at the top, and the colluvial soil at the bottom. The two types may be described as follows:

TYPE D. Eroded slope. This is an *in situ* soil, with weathering rock near the surface. Fig. 4 shows the profile of a typical pit (No. 3/656), which was described as follows:

0-20 cm. Medium brown fine sand with angular pieces of quartz and felspar. Merging.

20-35 cm. As above, but more quartz and felspar. Merging.

35-168 cm. (bottom of pit). Weathering coarse-grained granitic gneiss with a hard vein extending into the top layers.

TYPE E. Colluvial slope. This type consists of colluvial material containing some clay, overlying *in situ* rock. Fig. 4 shows the profile of a typical pit (No. 3/366), which was described as follows:

0 to 5-10 cm. Thin layers of dark grey and brown fine sand with clay. Well defined.

5-10 to 56-76 cm. Narrow bands of small loose rubble and finer sand; bands parallel to slope. Well defined.

56-76 to 63-76 cm. Pale brown clay. Well defined.

63-76 to 101-112 cm. Pale brown clay with sand. Merging.

101-112 to 137 cm. (bottom of pit). Pale brown clay-sand with felspar (*in situ* material).

It is evident that the eroded soil (Type D) is unfavourable to plant growth, whereas the colluvial soil (Type E) is relatively favourable as it contains down-washed clay which assists in water retention during the dry season.

(2) *Vegetation*

The density of vegetation on rocky slopes and hills depends basically upon the proportion of bare rock, and of eroded and colluvial types in the soil mosaic. Where bare rock is extensive the vegetation consists merely of isolated trees (with herbs and shrubs) in the crevices. Optimum development is found where there is a good proportion of colluvial material amongst the boulders. On steep slopes free from rocks most of the soil is badly eroded, and the vegetation is very poor open savanna.

The most significant features of the vegetation on rocky slopes and hills are: (a) the abundance of deciduous scandent shrubs which form a tangle understory; (b) the scarcity of grass; and (c) the protection that the rocks afford against fire and cattle. These features are interrelated and are of great importance in understanding the ecological status of the vegetation of the whole area (see p. 360).

Present-day farming practice shows that it is unlikely that rocky slopes and hills were ever cultivated, and field observations indicate that the rocks give some protection against fire. In the intensively used land by towns, such sites may be used for grazing goats and for providing fuel, but in more remote country it is very unlikely that either cattle or fuel cutters would bother about the rocky areas. It is therefore evident that such sites have suffered less disturbance than others.

Even small groups of boulders have their distinctive vegetation: one or two large trees (e.g. *Diospyros mespiliformis*, *Tamarindus indica* and *Ficus platyphylla*) draped with scandent shrubs. These clumps of dense vegetation appear as islands in the surrounding savanna.

Similar communities are developed on a larger scale on rocky slopes and hills. Several species are confined to these sites, such as *Boscia salicifolia* and *Isobertinia tomentosa* (a common species of the Guinea zone); a number of other Guinea zone species (e.g. *Pterocarpus erinaceus* and *Khaya senegalensis*) are found only on rocky hills and by water-courses.

Descriptions of two communities are given below. One community (Plot 2/168-268) is on a low rocky hill and the relatively large number of woody species (36), including several streamside species, suggests that the site is favourable. The other community is on a steep-sided hill (Dutsen Bagai), composed mostly of large boulders, and the paucity of species reflects the relatively poor soil conditions.

(a) *Anogeissus-Lannea microcarpa*, savanna woodland with deciduous tangles

Position: Line 2/168-268; area 0.4 ha.

Profile No. 3 (Fig. 5).

Soil: mosaic of boulders and colluvial soil (Type E) with a lesser amount of eroded soil (Type D).

Vegetation form: quite dense woodland, 7.5-9 m. high, abundant scandent deciduous shrubs, local thickets of small trees, little grass.

Floristic composition: *Anogeissus leiocarpa*, *Lannea microcarpa* and *Diospyros mespiliformis* are the dominant large trees; *Boscia salicifolia* and *Ficus glumosa* are less common but are very characteristic. *Combretum glutinosum*, *Dichrostachys glomerata* and *Commiphora pedunculata* are common small trees. *Combretum micranthum*, *Acacia ataxacantha* and *Strophanthus sarmentosus* are abundant as scandent shrubs and locally form impenetrable tangles; erect shrubs include *Guiera senegalensis* (l.f.), and *Ximenia americana* (f.).

Enumeration of trees:

Species	Girth in cm.											Total
	5-15	15-30	30-45	45-60	60-75	75-90	90-105	105-120	120-135	135-150	Over 150	
<i>Anogeissus leiocarpa</i>	1	3	3	9	1	5	1	2	.	1	1-150/165 3-165/180	30
<i>Lannea microcarpa</i>	1	4	2	.	.	8	1	1	.	.	.	17
<i>Diospyros mespiliformis</i>	6	3	.	2	.	2	13
<i>Boswellia dalzielii</i>	.	1	1	1	.	.	.	1	.	2	.	6
<i>Balanites aegyptiaca</i>	.	.	.	1	.	1	2
<i>Boscia salicifolia</i>	.	.	.	1	.	1	2
<i>Ficus glumosa</i>	1	.	1	.	.	.	2
<i>Sterculia setigera</i>	1	.	1	.	2
<i>Sclerocarya birrea</i>	1	1
<i>Tamarindus indica</i>	1	1
<i>Dichrostachys glomerata</i>	42	42
<i>Combretum glutinosum</i>	11	3	.	1	15
<i>Commiphora pedunculata</i>	11	1	12
<i>Annona senegalensis</i>	8	2	.	2	12
<i>Strychnos spinosa</i>	1	1	1	3	6
<i>Commiphora africana</i>	3	.	.	2	5
<i>Stereospermum kunthianum</i>	1	3	.	1	5
<i>Bridelia ferruginea</i>	2	.	1	.	1	4
<i>Lonchocarpus laxiflorus</i>	2	1	3
<i>Entada sudanica</i>	.	.	.	2	2
<i>Khaya senegalensis</i>	2	2
<i>Gymnosporia senegalensis</i>	.	.	1	1
<i>Lannea schimperi</i>	.	.	.	1	1
<i>Ximenia americana</i>	.	.	1	1
<i>Ziziphus mauritiana</i>	1	1
Total	92	22	10	26	2	20	2	6	.	4	4	188

Number of trees per hectare: 285 under 30 cm. girth
 185 over 30 cm. girth
 470 total

(b) *Deciduous tangles with emergent trees*

Position: Line 4; the hill Dutsen Bagai.

Profile No. 7 (Fig. 6).

Soil: boulders of extremely hard fine-grained garnetiferous quartzite, with equally hard Charnockite rocks near the base of steep slopes; with pockets of colluvial and eroded soil.

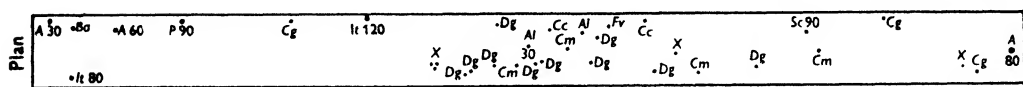
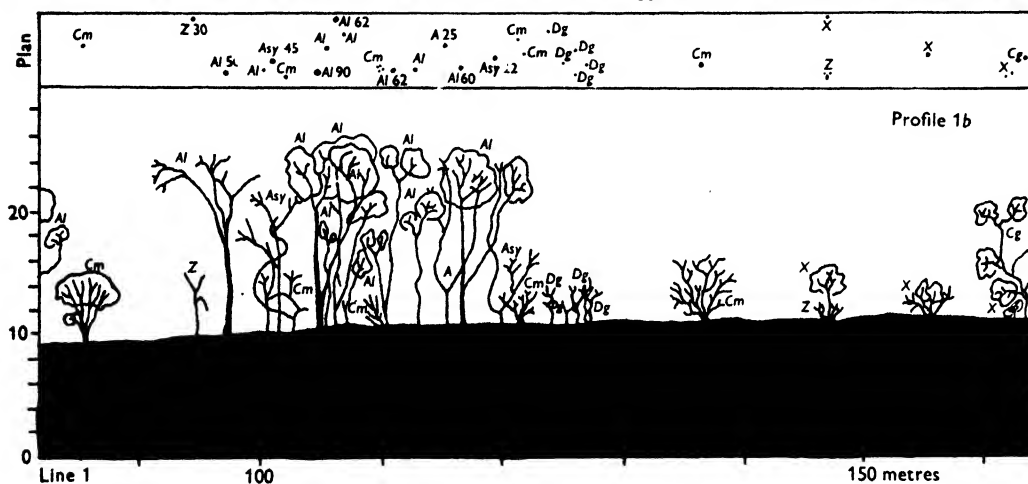
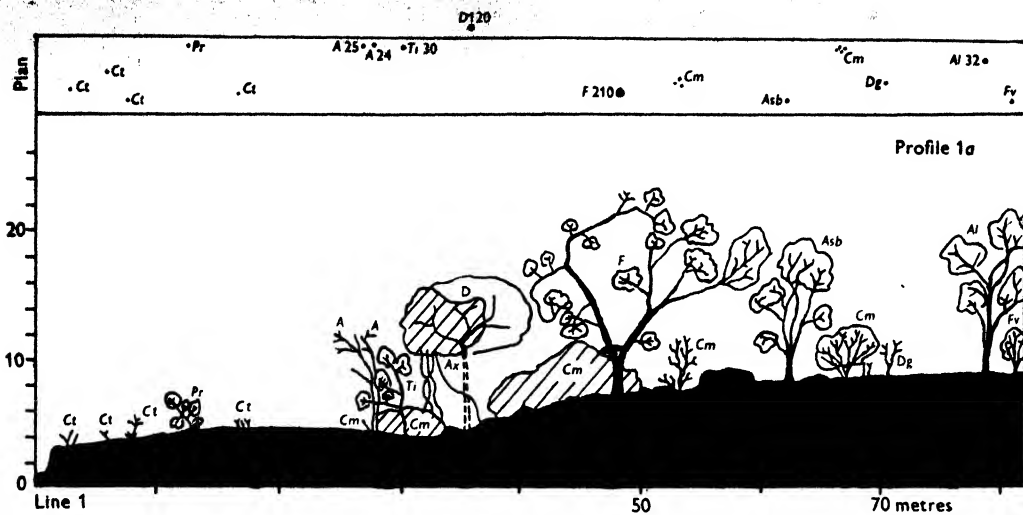
Vegetation form: almost continuous tangle, up to 4.5 m. high, with emergent upper stratum trees to 10 m. high; grass in open patches, unburnt.

Floristic composition: *Boswellia dalzielii* (f.), *Lannea schimperi*, *L. microcarpa*, *Boscia salicifolia*, *Sterculia setigera* and *Bombax* sp. as emergent trees, with *Sclerocarya birrea* at the bottom of the slope. Tangle of *Combretum micranthum*, *Acacia ataxacantha* and *Gardenia sokotensis*, with lower stratum trees of *Commiphora pedunculata* and *C. africana*. (No enumeration made.)

Low-level sites

(1) *Soils*

The degree of drainage is the important factor determining soil type in the low-level complex, as Morison *et al.* (1948) point out. By the River Fafara and its tributaries most of the soils are well drained, though small areas with impeded drainage also occur. Drainage is, however, seriously impeded in the shallow basins which form the sources of the tributaries. Fig. 7 is a map of a small tributary showing the shallow basin of ill-drained soil (Type F) at its source; similar sites with the same vegetation (*Acacia seyal* open savanna) may also occur along the course of a tributary, especially where two such streams meet. Fig. 3 is a diagrammatic section of the Fafara valley, showing the terraces on which two



types (Types G and H) of relatively well-drained soil are found. Sites near to the river are evidently better supplied with ground water during the dry season than those farther away.

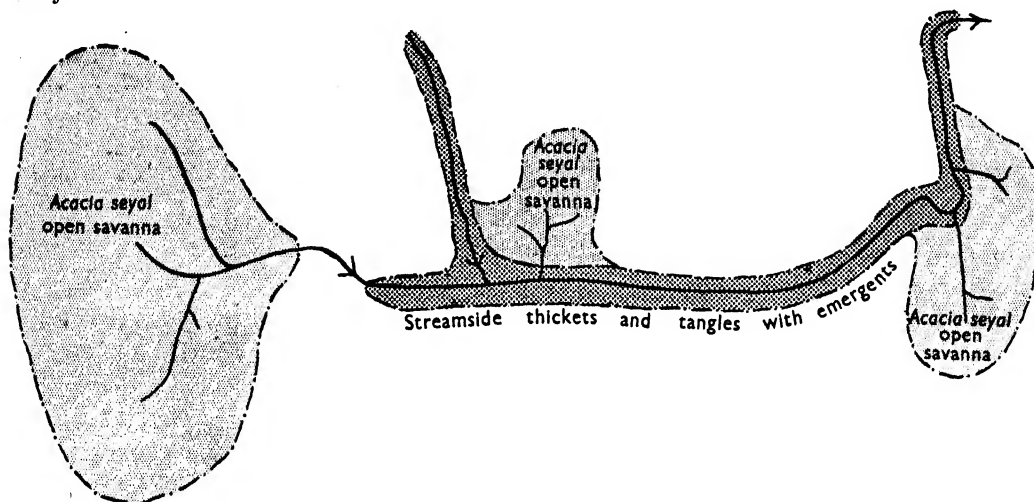


Fig. 7. Map of a stream's source showing position of *Acacia seyal* basins. The surrounding vegetation is *Combretum glutinosum*-*Lannea microcarpa* open savanna.

The low-level soils may be described as follows:

TYPE F. Semi-basin site silt. The essential features seem to be the surface layer of fine sand, the hard compacted subsurface layer of silt with orange-brown flecks and columnar structure, and the very sharply defined boundary between these layers. It is evidently the subsurface layer of compacted soil which impedes drainage sufficiently to make the surface flooded in heavy rain. When flooded, water drains off laterally to form tributary streams. Fig. 4 shows the profile of a typical pit (No. 2/1586) which was described as follows:

- 0 to 8-28 cm. Very pale grey-brown fine sand, with flecks of orange-brown in deeper parts. Well defined but at a varying depth.
- 8-28 to 25-46 cm. Grey-brown with orange-brown flecks, silt with some coarse sand, very hard, fissured into finely vesicular columnar pieces. Merging.
- 25-46 to 108 cm. Pale ochrous brown with orange-brown flecks, fine sand and silt, occasional angular pieces of quartz, manganese concretions below 60 cm., very hard, finely vesicular. Well defined.
- 108-119 cm. (bottom of pit). Hard weathering fine-grained granite.

TYPE G. Alluvial sand and gravel over weathering rock. Alluvial material has been deposited on *in situ* rock, which has since weathered to form sandy material. The soil is well drained but is supplied with ground water by the river. Fig. 4 shows the profile of a typical pit (No. 1/107) which was described as follows:

- 0-15 cm. Grey-brown fine sand. Merging.
- 15-46 cm. Red-brown gravel with rounded pebbles and a little clay. Merging.
- 46-168 cm. (bottom of pit). Sandy weathered gneiss.

TYPE H. Alluvial sand over clay with rock deep down. This is a deeper profile than Type G, containing clay instead of gravel and is not quite so freely drained. Fig. 4 shows the profile of a pit (No. 2/12) which was described as follows:

- 0-15 cm. Pale grey-brown fine sand, with water-worn pebbles. Merging.
- 15-125 cm. Pale brown sand. Merging.
- 125-153 cm. (bottom of pit). Pale ash-grey clay with sand.

(2) *Vegetation*

Tributaries start in shallow basins of silty soil (Type F) covered with *Acacia seyal* open savanna. Along the courses of the tributaries the riparian woodland consists of tangles and thickets with emergent trees. Near the main river the tributaries flow in steep gulleys filled with woodland which may be so rich in tangles as to be almost impenetrable. Terraces of the main river carry a mosaic of modified savanna communities, while the river banks themselves carry an irregular vegetation which includes very large isolated evergreen trees. In the dry season there are communities of annual herbs in the river bed itself. These low-level communities are described here in their topographical sequence.

(a) *Acacia seyal* open savanna. Almost pure communities of *A. seyal* occur right across the drier parts of tropical Africa. Usually they occur on heavy black soils in flat wide valleys, such as those described by Morison *et al.* (1948) at Aweil in the Anglo-Egyptian Sudan. Exactly similar communities are found in Nigeria in the wide valleys of the Hadejia-Katagum-Yobe river system. In Zamfara the river valleys are steep and narrow and such sites do not develop. *A. seyal* open savanna does, however, occur here at the sources of tributary streams. In both situations drainage is impeded so that water remains on the surface for some time before draining away laterally as run-off, directly to the main river in the Aweil sites, and into tributaries at Zamfara.

The occurrence of *A. seyal* in these two situations has an analogue in the moister Guinea zone. There *Terminalia macroptera* forms pure open savanna woodland both in low-lying riverain sites (just as Morison *et al.* (1948) found at Wau), and also in depressions at the sources of small streams.

The following is a description of a typical community in the shallow basin at the head of the stream shown in Fig. 7:

Position: Line 3/1860-1960; area 0.8 ha.

Profile No. 5 (Fig. 6).

Soil: Type F.

Vegetation form: open savanna woodland, almost entirely of lower stratum trees about 5 m. high, with occasional larger ones; regeneration thickets locally; isolated rounded shrubs of *Capparis corymbosa* up to 5 m. diameter on low mounds; grass to 0.5 m. high.

Floristic composition: *Acacia seyal* dominant; *Balanites aegyptiaca* (o.) is a very constant member of this type of community.

Enumeration of trees:

Species	Girth in cm.								Total
	5-15	15-30	30-45	45-60	60-75	75-90	90-105	105-120	
<i>Anogeissus leiocarpa</i>	4	.	1	.	.	.	1	1	8
<i>Lannea microcarpa</i>	.	.	1	.	2	.	1	.	5
<i>Acacia seyal</i>	65	40	33	1	10	4	2	.	155
<i>Balanites aegyptiaca</i>	1	2	4	.	2	11	.	.	20
<i>Dichrostachys glomerata</i>	4	4
<i>Sclerocarya birrea</i>	1	.	.	.	1	.	.	.	2
Total	75	42	39	1	15	15	4	1	194

Number of trees per hectare: 146 under 30 cm. girth
 96 over 30 cm. girth
 242 total

Regrowth shoots of tree species: *Acacia seyal* (f.).

It must not be supposed that *A. seyal* is confined to these semi-basin sites; indeed it was recorded in practically every enumeration plot. On high-level sites it is usually rare, but it becomes more frequent on lower-lying ground. It is also frequent in secondary vegetation on the rocky slopes above the river terraces in the Zurmi farmlands.

The varied colour of the bark of *A. seyal* is a remarkable feature. Many trees were examined, and it was found that the colour is connected with the shedding of bark scales. The scales are square or rectangular in shape and between 2 and 8 cm. in size. When still attached to the bole the scales are covered with red powder; later they separate off and leave a smooth green surface covered with yellow powder. Small grooves can be seen on the newly exposed surface; these become fissures and produce new scales which themselves become red and exfoliate. Sometimes some of the old scales do not fall off completely, especially at the base of the stem, and these go black.

Trees with exceptionally smooth stems covered with yellow powder have apparently just completed the shedding process, except for a few red or black scales which may remain near the base. As the bark fissures and forms scales so it becomes brown, and at the same time the powder changes from yellow to red. On very red trees the scales are usually ready to come off and can easily be removed to expose the smooth green surface below.

It seems that this process is repeated several times in the life of a tree. Trees of the same size may show the full range of colours. The period between shedding is not known and can only be determined by observing single trees for a number of years.

(b) *Streamside vegetation*. This consists of thickets of small trees, tangles of scandent shrubs, emergent larger trees, and open patches of tall grass. Several areas of such vegetation were examined by various streams and found to be constant in floristic composition. The following species are typical:

<i>Scandent shrubs and climbers forming tangles</i>	<i>Upper stratum trees as emergents</i>
<i>Capparis corymbosa</i>	<i>Diospyros mespiliformis</i>
<i>Combretum micranthum</i>	<i>Anogeissus leiocarpa</i>
<i>Acacia ataxacantha</i>	<i>Tamarindus indica</i>
<i>Leptadenia lancifolia</i>	<i>Lannea microcarpa</i>
	<i>Sclerocarya birrea</i>
<i>Lower stratum trees forming thickets</i>	<i>Ficus platyphylla</i>
<i>Dichrostachys glomerata</i>	<i>Balanites aegyptiaca</i>
<i>Commiphora pedunculata</i>	<i>Acacia sieberiana</i>
<i>Acacia seyal</i>	<i>A. campylacantha</i>
<i>Ximenia americana</i>	<i>Bombax</i> sp.
	<i>Butyrospermum parkii</i>
	<i>Adansonia digitata</i>
	<i>Albizzia chevalieri</i>

Near the main river the tributaries flow through steep-sided gulleys. The vegetation of such gulleys consists mainly of the species listed above, but is usually very thick and may form a closed canopy 10–15 m. high. Large dense tangles are extensive and anything up to 8 m. high.

(c) *River terrace communities*. It can safely be assumed that the vegetation of the river terraces in the Forest Reserve has grown up on farmlands similar to those of modern Zurmi. At Zurmi large trees are preserved on the river terrace farmlands, and patches of uncultivated vegetation remain in inaccessible rocky areas. Within the Reserve there are large trees which may well have stood in the farmlands a century or more ago. The most conspicuous of these are large evergreen *Khaya senegalensis*. One tree measured 4.75 m. in girth and about 28 m. high; the bole was very short (3.6 m.) but the huge crown was about 30 m. in diameter.

The best developed woodland communities on the river terraces to-day are: (i) riparian woodland, on rocky parts of the banks; (ii) *Albizzia chevalieri*, savanna woodland, on Type G soils; (iii) *Acacia campylacantha*, open savanna woodland, on Type H soils. Between these relatively well-developed communities are: (iv) open areas of tall grass, with shrubs and occasional large isolated trees; (v) thickets and climber tangles. These communities were described as follows:

(i) Riparian woodland (see Profile No. 1a in Fig. 5). The most frequent large trees are *Khaya senegalensis*, *Diospyros mespiliformis*, *Tamarindus indica*, *Ficus glumosa*, *F. gnaphalocarpa*, *Acacia sieberiana*, and *Adina microcephala* which usually grows on rocks, often actually in the river bed. Other characteristic trees are *Celtis integrifolia*, *Erythrina* sp., *Vitex doniana*, *Anogeissus leiocarpa*, *Albizzia chevalieri*, *Acacia albida*, *A. campylacantha* and *Kigelia africana*.

Some of these species are specifically riparian in this region; others, such as *Diospyros*, *Tamarindus*, *Ficus glumosa* and *Albizzia*, are also found on rocky slopes and hills. Except for the wide-ranging *Diospyros mespiliformis* and *Celtis integrifolia*, none of the typical plants of Sudan zone riparian woodland is a species of the Forest Regions. This is an important difference between the Sudan and the Guinea zone where the streamside forests are floristic outliers of the Forest Regions (see Keay, 1947). Another important difference is that the understory of Sudan zone riparian woodland consists of deciduous scandent shrubs (see list in (v) below), whereas evergreen forest shrubs and trees form the understory of the Guinea zone streamside forests.

(ii) *Albizzia chevalieri*, savanna woodland. This rather unusual community was sampled by an enumeration plot, thus:

Position: Line 1/77-137; just above a patch of riparian woodland on a rocky part of the river bank; area 0.24 ha.

Profile No. 1b (Fig. 5).

Soil: Type G.

Vegetation form: savanna woodland, with closed canopy; tall shrubs (3-5 m.) and occasional lianes reaching to tree tops; tangles and thickets in gaps; grass sparse.

Floristic composition: *Albizzia chevalieri* (dom.), *Combretum micranthum* (f.) as shrub and as liane; *Bauhinia rufescens* (o.), *Capparis corymbosa* (o.), and *Acacia ataxacantha* (o.) as scandent shrubs; *Dichrostachys glomerata* (l.d.) in thickets.

Enumeration of trees:

Species	Girth in cm.									Total
	5-15	15-30	30-45	45-60	60-75	75-90	90-105	105-120	Over 120	
<i>Albizzia chevalieri</i>	2	3	12	10	10	6	.	1	1-135/150	45
<i>Anogeissus leiocarpa</i>	1	3	1	4	1	1	.	.	1-165/180	13
<i>Acacia seyal</i>	1	.	3	4	.	1	.	1	.	10
<i>A. campylacantha</i>	2	.	.	.	2
<i>A. sieberiana</i>	1	1	.	2
<i>Lannea microcarpa</i>	.	.	.	1	.	1	.	.	.	2
<i>Balanites aegyptiaca</i>	.	.	1	.	.	1	.	.	.	2
<i>Commiphora pedunculata</i>	4	1	5
<i>Piliostigma reticulatum</i>	.	1	2	3
<i>Combretum glutinosum</i>	.	3	3
<i>Sclerocarya birrea</i>	.	.	1	1
<i>Tamarindus indica</i>	.	.	1	1
<i>Ziziphus mauritiana</i>	.	.	1	1
Total	8	11	22	19	11	12	2	3	2	90

Number of trees per hectare: 79 under 30 cm. girth
296 over 30 cm. girth
375 total

Regrowth shoots of tree species: *Dichrostachys glomerata* (l.a.).

(iii) *Acacia campylacantha*, open savanna woodland. In places *A. campylacantha* grows almost pure and forms good open woodland 12–15 m. high. In other, more disturbed, areas it is mixed in open savanna with species such as *A. sieberiana*, *Piliostigma reticulatum*, and very rarely with the Guinean species *Terminalia glaucescens*. Well-marked communities of *Acacia campylacantha* appear to be associated with soils of Type H (alluvial sand over clay with rock deep down).

(iv) Open areas of tall grass, with shrubs and occasional large isolated trees. The river terraces provide attractive farmland, and it is obvious that they have been cultivated spasmodically since the area was depopulated. It appears that these open areas of irregular vegetation are regrowth on relatively recently abandoned farmland. Plants commonly seen in these seral communities include:

<i>Ziziphus mauritiana</i>	<i>Annona senegalensis</i>
<i>Piliostigma reticulatum</i>	<i>Fluggea virosa</i>
<i>Calotropis procera</i> *	<i>Vernonia amygdalina</i> *
<i>Jatropha curcas</i> *	<i>Ricinus communis</i> *
<i>Cassia tora</i> *	<i>Leonotis africana</i> *

Such vegetation has much in common with that of waste ground around villages. The species marked (*) are characteristic ruderal and semi-cultivated plants.

(v) Thickets and climber tangles. Dense thickets of *Dichrostachys glomerata* are characteristic of the sandy parts of the river bank and appear to be an early regrowth stage after the bank has been cleared of its vegetation, either by animals going down to the river to drink, or else by the action of the river itself. *Commiphora pedunculata* forms similar thickets less commonly. Huge tangles of deciduous scandent shrubs are composed of *Acacia ataxacantha*, *Combretum micranthum*, *Bauhinia rufescens*, *Ziziphus mucronata*, *Capparis corymbosa* and *Mimosa pigra*.

(d) The river bed. Rocks which are overwhelmed in flood but remain above the water most of the year are covered with thickets of *Phyllanthus beillei* and occasional trees, such as *Adina microcephala* and *Acacia albida*. As the river dries up, the sandy parts support an open vegetation of annual herbs. One of the most frequent of these herbs is *Glinus lotoides*, whose dense mat of white woolly leaves often covers quite a large area (up to 1 m. diam.).

Old village sites

The vegetation and soils on the sites of two deserted villages were examined. These villages, Bagai and Matuzgi, were deserted in the troublous times of last century, probably between 1850 and 1870.

The village of Bagai was on sandy soil (Type B), below a rocky hill. There are no remains of the houses and the site is now covered by woodland 9–11 m. high, composed almost entirely of *Anogeissus*. Grass is not dense but is evenly spaced and tall; in May it was still unburnt. It seems reasonable to suppose that *Anogeissus*, with *Dichrostachys*, invaded the deserted site and was favoured by the protection from fire that the bare ground would have afforded (cf. Segregate I on p. 349).

The village of Matuzgi is on the rocky slope above the river terrace. Large earthenware dye pots sunk in the ground are all that remains of the village. Irregular savanna of *Acacia seyal* now covers the site.

A remarkable feature of both these sites is the colour of the soil. In the area as a whole the soil is seldom at all red in colour, and red lateritic loam and concretionary ironstone are altogether lacking.

There is a similar absence of red soils and lateritic concretions in the sands of the Chad Group of north-eastern Nigeria. The reason for this absence is probably the same in both areas, namely, the extremely porous nature of the parent material, whether it be deep sands of the Chad Group or porous weathered gneiss overlain by sandy drift.

Thomas (1946) has written about the influence of human habitation on soils in Uganda. He suggests that the occurrence of red earths and lateritic ironstone is correlated with former human settlement. In Nigeria large tracts of red earths and lateritic ironstone have undoubtedly been formed quite independently of human interference. It is, however, interesting to note that in the Zurmi area red earths have been found on the sites of two deserted villages, while all around the high-level and slope soils are of a grey-brown or yellow-brown colour.

V. ECOLOGICAL STATUS

In trying to determine the climatic climax of this region it would be desirable to examine undisturbed communities on the high-level site. The high-level site, as Morison *et al.* (1948) point out, represents the climatic normal in the sense that the soil receives neither water nor dissolved nor suspended matter from other areas. In the Zurmi area, however, the vegetation of high-level sites is greatly disturbed, having been cultivated up to about 90 years ago and still being influenced by grass fire and cattle. These biotic influences are not uniform throughout the area, either in kind or in time, and the vegetation is consequently an extremely complicated mosaic of numerous secondary seral communities at various stages of development and influenced by various biotic factors or combinations of factors. This biotic complex is superimposed on an almost equally complex mosaic of soil types which may vary considerably in quite small areas. Under these influences the dominant species are segregated into communities of equal rank comparable to Braun's *associes-segregates* (Braun, 1935). Seral development within each segregate may be recognized (e.g. *Anogeissus-Dichrostachys* thickets develop into *Anogeissus* woodland), but the communities of the whole high-level complex are not arranged in a single sere leading to one climax.

Chevalier (1933) recognized the secondary nature of most Sudan zone vegetation, and stated that relics of the primitive vegetation are now found only on uncultivable rocky plateaux and stony hills and along water-courses. In the Zurmi area it is clear that the most undisturbed vegetation is to-day found on rocky hills and slopes. The river terraces are much disturbed but the small streams probably less so. A streamside is, however, more favourable as regards water supply than the high-level complex, so its vegetation cannot be equivalent. The most likely places to seek vegetation approximating to the climatic climax is, therefore, rocky hills, steep and rocky enough to afford protection from cultivation, fire and cattle, but not so steep and rocky as to be quite different from the normal high-level site.

A good example of such vegetation was found on the low rocky hill described on p. 353. The features of this vegetation are: (i) *form*, dense savanna woodland; (ii) abundant deciduous scandent shrubs; (iii) grass only local; (iv) relatively numerous woody species; (v) *Anogeissus* not overwhelmingly dominant, several other species (e.g. *Lannea microcarpa*) being frequent in the upper stratum; (vi) *Combretum glutinosum* and *Strychnos spinosa*, both frequent but not overwhelmingly dominant in the lower stratum.

Such a low rocky hill is naturally a little more favourable than the ordinary high-level site, as the presence of such trees as *Diospyros* and *Khaya* indicates, but it seems that the

vegetation does approximate to what may be the climatic climax of the area as a whole.

This hypothesis is supported by a study of vegetation in other parts of Africa with similar climate and soil. Hoyle (verbal communication) informs me that vegetation approximating to that of the rocky hill described above occurs on ordinary high-level sites in the Anglo-Egyptian Sudan in country north of the Aweil area to which reference has already been made (Morison *et al.* 1948).

In 1947 I paid a short visit to the Sheseke District of Northern Rhodesia, about 100 km. west of the Victoria Falls. A distinct type of vegetation known as 'mutemwa' occurs there to the south of the *Isoperlinia-Brachystegia* woodlands (similar to the Northern Guinea zone of Nigeria). The climate of this area is similar to that of the Sudan zone in Nigeria, although dry-season minimum temperatures are lower. As in Nigeria, the land is covered by a deep drift of desert sand laid down in a dry Quaternary period; unlike Nigeria, however, this area has hitherto been sparsely populated and the vegetation still approximates to the virgin state. In 'mutemwa' vegetation there is a dense tangled understory of erect and scandent deciduous shrubs (e.g. *Dalbergia glandulosa*, *Combretum* spp.) which almost completely excludes grass. The upper stratum trees are up to 20 m. high, and in places form a closed canopy, but usually are more widely spaced; typical species are *Baikiaea plurijuga* and *Pterocarpus stevensonii*. If fire enters, the underwood burns fiercely and is subsequently replaced by grass, and the 'mutemwa' gradually changes to open savanna very like that of the Sudan zone in Nigeria.

All this suggests that the climax vegetation of the Zurmi area consisted of a dense understory of deciduous dry-zone shrubs and lower stratum trees with upper stratum trees forming a rather open canopy. Although in itself stable, such vegetation would obviously be quickly destroyed once fires started, and would become degraded to an open savanna type with grass dominant. This is happening in Sheseke to-day, but may well have happened in Nigeria long ago. Further research may, however, indicate that the Zurmi area has been inhabited throughout the present climatic era, and that the vegetation has never been allowed to attain its climatic climax over continuous areas. Certainly to-day, ecological studies in the Sudan zone of Nigeria must consist largely of unravelling the varied effects of many kinds of biotic disturbance.

VI. SUMMARY

Practically no ecological work has hitherto been done near the northern boundary of Nigeria, a region which has attracted attention in connexion with the alleged encroachment of the Sahara. An ecological investigation was therefore made near Zurmi in the Zamfara Forest Reserve, Sokoto Province, in April and May 1946.

The vegetation here was taken as an example of Chevalier's Sudan zone (Chevalier, 1933, *et al.*). The most widespread type in this zone to-day is open savanna or open savanna woodland, with fine-leaved and broad-leaved trees in roughly equal proportions, together with a fair number of thorny species. Practically all the trees and shrubs are deciduous for several weeks.

Morison *et al.* (1948) described similar vegetation in the Anglo-Egyptian Sudan, their Aweil transect corresponding closely to parts of the Sudan zone in Nigeria. In the Aweil transect the low-level complex is extensive, but in the Zurmi area it is the high-level complex which comprises most of the regional ecosystem.

On high-level sites a sandy drift of varying thickness covers *in situ* weathering granites and gneisses, sometimes with an intervening clay-rubble layer. The clay-rubble layer retains a certain amount of water in the dry season, and is therefore of great importance to the vegetation in this dry area (mean annual rainfall about 710 mm.; October to April with less than 2 mm. rain per month, and mean monthly 3 p.m. relative humidity less than 30%).

Historical records show that the area examined was well cultivated up to about 1860, but has since been very sparsely populated. Most of the vegetation is therefore secondary regrowth. To-day grass fires and cattle are the important biotic factors. The grass fires tend to keep the vegetation open, eliminate certain species and hence selectively to favour fire-resistant species especially *Combretum glutinosum* and *Strychnos spinosa*. The cattle trample and graze the herb layer thus stopping fires, not only in directly affected areas, but also in areas surrounded by trampled 'fire-breaks'. This protection from fire favours the regeneration of trees, particularly *Anogeissus leiocarpa*, whose foliage is distasteful to cattle.

The abundance of the three most frequent trees (*A. leiocarpa*, *Combretum glutinosum* and *Strychnos spinosa*) is affected by soil conditions as well as biotic factors. Soils with the water-retaining clay-rubble layer (Type A) evidently favour *Anogeissus*, whereas *Combretum* and *Strychnos* tend to dominate on the drier sandy soils (Types B and C).

The complex action of the soil mosaic and the two main biotic factors upon the vegetation of high-level sites is best understood by considering first an 'ideal' mesic community in which *Anogeissus*, *Combretum* and *Strychnos* are codominants. Such a community exists under what appear to be mesic conditions of soil and minimum biotic disturbance. Under the influence of more extreme edaphic and biotic factors the three dominants segregate to form communities comparable to Braun's (1935) *association-segregates*. The four main segregates are:

Segregate I: soil, Type A; biotic factor, cattle. *Anogeissus*, open savanna woodland with regeneration thickets.

Segregate II: soil, Type A; biotic factor, fire. *Combretum-Strychnos*, open savanna; a few large *Anogeissus* but no regeneration thickets.

Segregate III: soil, Type B; biotic factor, cattle. *Anogeissus-Combretum-Strychnos*, open savanna woodland with *Anogeissus* regeneration thickets.

Segregate IV: soil, Type B; biotic factor, fire. *Combretum-Strychnos* open savanna.

The biotic factors change from time to time, both in kind and intensity, so that communities transitional between Segregate I and II, and between III and IV may occur.

Seral development within each segregate is recognizable, but the segregates are not arranged in a single sere leading to one climax, and must be regarded as equal in rank.

Vegetation on low-level sites includes: (a) *Acacia seyal*, open savanna in shallow basins which are the sources of tributary streams; (b) streamside thickets and tangles with emergent trees; and (c) a complicated mosaic of biotically modified communities on the river terraces.

On rocky slopes and hills the vegetation is less modified. The rocks prevent cultivation and also, to a certain extent, fires and trampling by cattle. The vegetation of such sites often has a dense understory of deciduous erect and scandent shrubs which limit grass to occasional open patches.

The problem of determining the climatic climax is by no means easy, but the vegetation

of low rocky hills suggests an answer which is corroborated by observations in other parts of Africa. The climax appears from this evidence to be deciduous woodland with a dense understory of erect and scandent shrubs and only occasional patches of grass. Biotic influences have turned this into open savanna with grass dominant below widely spaced trees. It is, however, quite possible that these influences are so ancient and widespread that the climax has never been allowed to develop properly during the present climatic era.

In conclusion I wish to thank Mr A. C. Hoyle of Oxford, and Mr J. P. M. Brennan of Kew for assistance in naming certain plants and for many constructive criticisms, as well as Mr S. B. Williams and students of the Ibadan Forest School who assisted in the field work.

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APPENDIX

LIST OF WOODY SPECIES RECORDED IN THE ZURMI AREA

The numbers in brackets refer to specimens collected during April and May 1946; numbers in italics were collected by me personally, others by students of the Ibadan Forest School. All are Forest Herbarium Ibadan (FHI) collecting numbers.

ANNONACEAE

Annona senegalensis Pers. (16192)

CAPPARIDACEAE

Maerua crassifolia Forsk. (16182)

Capparis corymbosa Lam. (16119)

Boscia salicifolia Oliv. (16165)

POLYGALACEAE

Securidaca longepedunculata Fresen. (15700)

COCHLOSPERMACEAE

Cochlospermum tinctorium A. Rich.

COMBRETACEAE

Combretum nigricans Lepr. var. *elliottii* (Engl. & Diels) Aubreville (16173, 16176)

C. glutinosum Perr.; syn. *C. passargei* Engl. & Diels; the name *C. verticillatum* has been used wrongly for this species (16118, 16139, 16153-7, 16163, 16183, 16203)

C. micranthum G. Don (15665)

C. velutinum DC.; syn. *C. sokodense* Engl. (16140, 16148, 16185)

- Guiera senegalensis* Lam. (18031)
Terminalia avicennioides Guill. & Perr. (16134)
T. glaucescens Planch.
Anogeissus leiocarpa Guill. & Perr. (16151)
- TILIACEAE**
Grewia mollis Juss. (16198)
- STERCULIACEAE**
Sterculia setigera Del. (15815)
- BOMBACACEAE**
Adansonia digitata Linn.
Bombax sp. (16175)
- EUPHORBIACEAE**
Bridelia ferruginea Benth.
Phyllanthus beillei Hutch.
Fluggea virosa Baill.
Jatropha curcas Linn.
Chrozophora brocchiana Vis. (15685)
Ricinus communis Linn.
- CAESALPINIACEAE**
Bauhinia rufescens Lam. (16129)
Tamarindus indica Linn. (16177)
Cassia mimosoides Linn.
C. sieberiana DC. (16135)
C. aschrek Forsk. (15667)
C. singueana Del.
C. tora Linn.
Isobertlinia tomentosa (Harms) Craib & Stapf (16141)
Piliostigma reticulatum (DC.) Hochst.; syn.
Bauhinia reticulata DC. (16161)
- MIMOSACEAE**
Parkia oliveri Macbride (16205)
Entada sudanica Schweinf. (16133)
Prosopis africana Taub. (16179)
Dichrostachys glomerata (Forsk.) Chiov. (15868)
Mimosa pigra Mill. (15894)
Acacia albida Del. (15670)
A. arabica Willd. (*A. scorpioides* (L.) A. Chev.) (15666)
A. ataxacantha DC.
A. campylacantha Hochst. ex A. Rich. (15897, 16202)
A. macrostachya Reichenb. ex Benth.
A. senegal Willd. sensu stricto, non *A. dudgeoni* Craib (16145, 16169)
A. seyal Del.; syn. *A. stenocarpa* Hochst.; non *A. seyal* of A. Chev., non *A. seyal* var. *multijuga* Schweinf. (16180)
A. sieberiana DC. (16136) (and var. *villosa* A. Chev.)
Albizzia chevalieri Harms (16127)
- PAPILIONACEAE**
Pterocarpus erinaceus Poir. (16164)
Ostryoderris chevalieri Dunn (16172)
Lonchocarpus laxiflorus Guill. & Perr. (16162)
Erythrina sp. (16190)
Abrus precatorius Linn.
- ULMACEAE**
Celtis integrifolia Lam. (16188)
- MORACEAE**
Ficus gnaphalocarpa A. Rich. (16122)
F. glumosa Del. (16123, 16171)
F. glumosa Del. var. *glaberrima* Martelli (16160)
F. basarensis Warb. (16115)
Ficus sp. ? *leonensis* Hutch. (16116)
Ficus sp. (16178)
- CELASTRACEAE**
Gymnosporia senegalensis Loes. (sensu lato) (16195)
- OLACACEAE**
Ximenia americana Linn. (15610)
- LORANTHACEAE**
Loranthus globiferus var. *verrucosus* Sprague (16120)
L. tambermensis Engl. & Krausse (16174)
- RHAMNACEAE**
Ziziphus spina-christi Willd.
Z. mucronata Willd.
Z. mauritiana Lam. (16149)
- SIMAROUBACEAE**
Balanites aegyptiaca Del. (15668)
- BURSERACEAE**
Boswellia dalzielii Hutch. (16152)
Commiphora pedunculata (Kotschy & Peyr.) Engl. (16150)
C. africana (A. Rich.) Engl.
- MELIACEAE**
Khaya senegalensis A. Juss. (16168)
- ANACARDIACEAE**
Sclerocarya birrea Hochst. (16126, 16158)
Lannea microcarpa Engl. & Krausse (16130, 16131, 16132)
L. schimperi (Hochst.) Engl. (16184)
Heeria insignis (Del.) O. Ktze. (16144)
- EBENACEAE**
Diospyros mespiliformis Hochst. (15673)
- SAPOTACEAE**
Butyrospermum parkii Kotschy
- LOGANIACEAE**
Strychnos spinosa Lam. (16159)
- APOCYNACEAE**
Strophanthus sarmentosus A.P. DC.
- RUBIACEAE**
Crossopteryx febrifuga Benth. (18016)
Macrosphyra longistyla Hook. f. (16128)
Gardenia erubescens Stapf & Hutch.
G. sokotensis Hutch. (16181)
Randia nilotica Stapf
Feretia canthioides Hiern
Adina microcephala Hiern (16137)
- BIGNONIACEAE**
Kigelia africana Benth. (16187)
Stereospermum kunthianum Cham. (15637)
- VERBENACEAE**
Vitex doniana Sw. (15850)
- PALMAE**
Borassus aethiopum Mart.
Hyphaene thebaica Mart.

ARBUTUS UNEDO

By J. ROBERT SEALY

*The Herbarium, Royal Botanic Gardens, Kew**(With Plates 9–11, and six Figures in the Text)*

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ARBUTUS UNEDO AT KILLARNEY*Introduction*

The Killarney lakes are sheltered from the prevailing south-west wind by mountains (up to 2750 ft. high) which encircle them on the south and south-west, completely enclosing the Upper Lake and Long Range. The latter is the stream which connects the Upper Lake to Muckcross Lake and Lower Lake (Lough Leane), the two latter being separated by a stretch of land broken through near its western end at Brickeen (Fig. 1).

The natural climax vegetation of the lowland area north of the mountains is evidently oakwood, but much of the land is now cultivated, and such woodland as exists is planted. On Ross Island—really a peninsula jutting into Lough Leane from the east—on the land between that lake and Muckcross Lake, and on the lower slopes of the mountains round the lakes, the ground is mostly too rocky and too steep for cultivation, and these areas are largely covered by woodland, much of which is believed to be natural (Praeger, 1934). The dominant tree is *Quercus petraea* (Matt.) L. ex Lieblein (*Q. sessiliflora* Salisb.) and the climax vegetation is oakwood. An account of the latter has been given by Turner & Watt (1939) and by Tansley (1939). In general its distribution is limited to areas where there is sufficient shelter from the south-west wind.

At Killarney *Arbutus unedo* is pre-eminently an inhabitant of cliffs and open rocky slopes, and though often found at the margins of oakwoods, it is very rarely a constituent of them, and is never found in the fully developed climax woodland, such as that on the

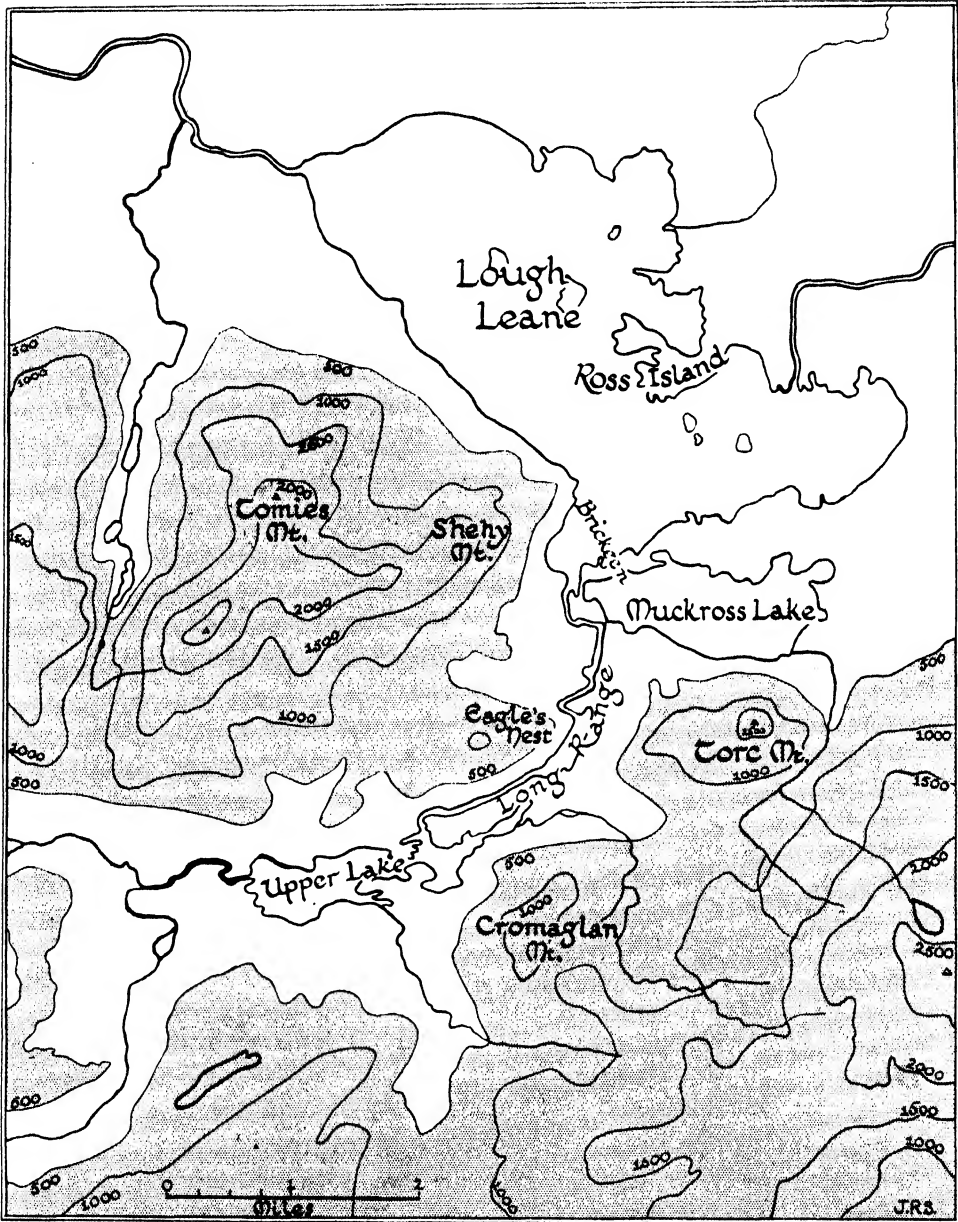


Fig. 1. Map of the Killarney lakes and adjacent mountains, based on the Ordnance Survey map, 1 in. to 1 mile.

north-eastern slopes of Tomies and Shehy Mountains above Lough Leane and that south of the Upper Lake. Around Lough Leane and Muckcross Lake the rock is Carboniferous Limestone, and here the *Arbutus* was growing in 'soils' of pH 4.5–6.5 or 7. In the southern part of the region the rock is Old Red Sandstone and the pH was generally 4–4.5. It will be convenient to describe the occurrence of the *Arbutus* under four headings, viz.:

Limestone cliffs and rocky areas around Muckcross Lake and Lough Leane.

Woodland between Muckcross Lake and Lough Leane.

Sandstone cliffs and outcrops around the Long Range and Upper Lake.

Mountain slopes.

On limestone cliffs and rocky areas of Lough Leane and Muckcross Lake

The coasts of the islands in Lough Leane, of Ross Island, and of the southern shore of Lough Leane, as well as much of the coast of Muckcross Lake, are limestone cliffs up to 30–40 ft. high. These, and also the rocky areas above them which are not covered by woodland, support an open shrub-vegetation of which *Arbutus unedo* is the chief constituent. Characteristically, the plants are dense bushes 3–12 ft. high, but all stages are represented from tiny seedlings to trees over 30 ft. high. They grow in the clefts and fissures of the rock, and obviously thrive in such places, their principal associates being *Taxus baccata* L. and *Ilex aquifolium* L. The cliffs proper may be bare except for scattered plants of *Arbutus* and *Taxus*, or the vegetation may be more or less continuous with bushes and trees of *Arbutus* 1–30 ft. high associated with *Taxus* (also often quite large), *Ilex* and *Sorbus aucuparia* L. Quite often the woodland extends to the cliff-edge, and *Arbutus* is found at the margin, the plants varying from small shrubs 2½ ft. high to trees up to 30 ft. Where the woodland does not reach the cliff-edge, the intermediate area is usually more or less bare rock with vegetation at various stages of development. Here and there the rock is bare except for a few herbs in the fissures, or it may be but sparsely covered by prostrate or creeping plants, low herbs and small shrubs. In one such area *Clematis vitalba* L. was abundant, with *Rubus fruticosus* (aggr.), *Taxus*, *Prunus spinosa* L. and the procumbent alien *Cotoneaster microphylla* Lindl. as the other principal species--the *Prunus* had stout stems 9–10 in. deep in the rock-crevices and branches spreading out close to the rock-surface, while the *Taxus* specimens were similar or more erect and bushy; in addition, there were scattered plants of *Arbutus*, *Sorbus rupicola* (Syme) Hedl., *Sorbus aucuparia* L. *Corylus avellana* L., *Succisa pratensis* Moench., *Teucrium scorodonia* L., *Rosa spinosissima* L. and *Rubia peregrina* L. More often the shrubs are taller, and a typical example had *Arbutus* (2–12 ft. high) and *Taxus* as the principal constituents, accompanied by *Ilex*, *Corylus avellana*, *Sorbus aucuparia* and *S. rupicola*; the ground cover, which was open to thinly subcontinuous, consisted of *Ulex gallii* Planch., *Thymus serpyllum* L., *Clematis vitalba*, *Rubia peregrina* L., *Calluna vulgaris* (L.) Hull, *Erica cinerea* L., *Rosa spinosissima* L., *Hedera helix* L., *Carex flacca* Schreb. and various grasses and mosses. A further development is to be seen in areas where the shrubs are larger and still more prominent; in such areas the *Arbutus* is plentiful, 6–18 ft. high, and is accompanied by *Taxus* of the same size, the ground layer is discontinuous and may contain *Solidago virga-aurea* L. and *Leontodon autumnalis* L. in addition to the species mentioned above. A part (50 ft. long and 30 ft. wide) of one such area contained ten shrubs of *Arbutus* and four of *Taxus*, all 12–18 ft. high, several smaller plants of *Ilex*, one *Betula pubescens* and one *Corylus*, both 3 ft. high, a poorly developed *Corylus* and a straggly *Ulex europaeus* L.; the humus beneath the

Arbutus was 1–2 in. deep and contained a high proportion of *Arbutus* leaves. There seems no reason why the rocky areas between the present woodland and the cliff-edge should not eventually be covered by woodland, if the vegetation is allowed to develop naturally, and the examples given above seem to be transition stages. The existence of these is probably due to the cutting and clearing of the woodland. An example of this was seen, and the felled area, from which the trunks had not yet been removed, was completely covered by *Pteridium*. Felled areas are not replanted, the vegetation being left to regenerate naturally, and in exposed places the clearing of the woodland must often be followed by soil erosion—owing to the heavy rainfall (55 in. per year)—and the exposure of the underlying rock. Finally, mention must be made of certain rocky bluffs in the coasts of the lakes, which are covered by a dense growth of *Calluna*, with some *Pteridium* and *Ulex*, and which also support a scrub of *Arbutus* and *Ilex*. On one of these bluffs the *Arbutus* specimens were from 12 to 20 ft. high (most of them 15 ft.), and were accompanied by only one or two plants of *Ilex* (Pl. 11, phot. 5).

In the woodland between Lough Leane and Muckcross Lake

Much of the land which separates Lough Leane and Muckcross Lake is wooded, and in general the dominant tree is *Quercus petraea* (*Q. sessiliflora*). Sometimes it is the sole tree with *Ilex* forming a shrub-layer, and with virtually no ground cover. More often it is the dominant in mixed woodland, being accompanied by *Fraxinus excelsa*, *Sorbus aucuparia*, *Taxus baccata*, and *Betula*, with the shrub-layer formed of *Taxus*, *Corylus*, *Rhododendron ponticum* and *Ilex*, either singly or in combination, while the ground-layer may comprise one or more of *Calluna*, *Vaccinium myrtillus*, *Ilex*, *Pteridium* and *Rubus fruticosus*. Occasionally old trees of *Arbutus*, generally 30–40 ft. high* (i.e. as high as the oaks), are to be found growing singly, or two or three together, some distance inside the woods.

In some areas, however, the *Arbutus* forms part of the woodland and may be co-dominant with *Quercus*, or even dominant in some places. In such instances the *Arbutus* are always large trees, 30 ft. or more in height, and 3 ft. or more in girth†; *Ilex* usually forms the shrub-layer, though *Rhododendron* may also be present.

Near Brickeen Bridge large trees of *Arbutus* are a feature of a very open woodland, which includes also a few small trees of *Sorbus aucuparia*, *Ilex*, *Betula*, *Populus tremula*, *Quercus* and *Rhododendron*; the ground is very rocky, and between the rocks are growths of *Calluna* and *Pteridium*. North-eastwards this passes into a mixed woodland of *Taxus*, *Arbutus*, *Ilex*, *Betula* and *Quercus*, the trees all rather more than 20 ft. high; dense *Rhododendron* thickets form much of the undergrowth. This passes into more open woods with taller trees (30–40 ft. high), in parts of which *Arbutus* forms almost pure stands; *Ilex* and *Rhododendron* (especially the latter) form the shrub-layer, and a few small trees of *Sorbus*

* Examples measured were: 30 ft. high, trunk cylindrical and unbranched for 5½ ft., 3 ft. to 3 ft. 2 in. in girth; 40 ft. high, trunk 4 ft. in girth at 3 ft. from the ground and unbranched for 10½ ft.; 30 ft. high, 3 ft. in girth; 30 ft. high, 8 ft. in girth close to the ground and there divided into three trunks, respectively 4 ft. 8 in., 4 ft. and 2 ft. 6 in. in girth, which divide again to give in all ten fair-size ascending-spreading limbs; 40 ft. high, dividing close to the base into four trunks, 2 ft. 9 in., 3 ft. 3 in., 3 ft. 6 in. and 3 ft. 6 in. in girth. Calculations from the annual rings of sections of smaller trees, indicate that these large trees must be 200–300 years old.

† One tree was 6 ft. 7 in. in girth at 3 ft. from the ground, and the trunk was 11 ft. high before it forked—exceptional for *Arbutus*, which normally divides into two to four trunks quite close to the ground.

aucuparia are present in the more open places. The *Arbutus* trees are all big, and there are numerous dead and fallen specimens in the woodland—a typical example measured 38 ft. 9 in. in length, while another was over 33 ft. long and measured 9 ft. 8 in. in girth in the lowest 3 ft., above which it divided into two huge limbs. Here and there the woodland is traversed by flat-bottomed gullies which run down to the shore of Lough Leane, and it is interesting to note that while *Quercus* was growing on the flat bottoms of these gullies as well as on their rocky sides, *Arbutus* was confined to the latter. It was evident that *Arbutus* is dying out in these woods, which are becoming an association of *Quercus*, *Betula*, *Ilex*, and *Rhododendron*. No regeneration of *Arbutus* was observed in woodland (either here or anywhere else); no seedlings or young plants were seen, nor was there any regeneration by new shoots developing from the base of an old and fallen tree, though this is a not uncommon phenomenon in open habitats.

The presence of *Arbutus* in the woodland is doubtless due to natural regeneration after cutting. Though the area forms part of the Muckcross demesne, there has been little planting, and even that has been confined for the most part to exotic species which have been introduced here and there along the road which passes through the area. As already mentioned, a certain amount of cutting is done and apparently the felled area is left to regenerate naturally. It is evident from Smith's *History of Kerry* (1756) that two centuries ago the *Arbutus* was much more plentiful in the Killarney area than it is now, and that much of the woodland was cut to provide charcoal for smelting the silver, lead and copper that was mined there. This cutting had started fifty years before Smith published his *History*, for Molyneux wrote in 1697 (abridged 1809) about the *Arbutus* as follows: '... in the rocky parts of the county of Kerry, about Loughlane, and in the islands of the same lough, ... it flourishes naturally to that degree as to become a large tall tree; the trunks of these are frequently $4\frac{1}{2}$ feet in circumference, or 18 inches in diameter, and the trees grow to about 9 or 10 yards in height; and in such plenty that they now cut them down as the chief fuel to melt and refine the ore of the silver and lead mine, lately discovered near the castle of Ross, in the county of Kerry.' Now in the area between Lough Leane and Muckcross Lake there were copper mines, and there can be little doubt that the woodland in the area would have been cut for fuel for smelting. If this be correct, then the *Arbutus* now existing in the present woodland may be the plants which re-colonized the area, a possibility which is supported by the fact that the large trees now existing are believed to be 200–300 years old. It is highly probable that the cutting of the trees for smelting purposes would mean the virtual destruction of the woodland, which would almost certainly have been followed by extensive soil erosion and the exposure of the underlying rock. From the conditions observable in the same area to-day, it is probable that regeneration proceeded on the following lines. The bare rocky areas would be early colonized by *Arbutus* and *Taxus*, with perhaps a few plants of *Ilex* and *Betula*, and would in the course of a few years become covered with a shrub association of which *Arbutus* would be the chief constituent. As *Arbutus* cannot tolerate shading, plants growing in close stands would tend to grow upwards to form trees, instead of remaining as shrubs, and the same happens when they grow in company with *Quercus*. Except on the cliffs much of the terrain is suitable for oakwood, and once the shrub-communities are well established they are invaded by *Quercus*. In competition for light, *Arbutus* plants grow into trees along with *Quercus* (as they do when growing in close pure stands), reaching a height of 30–40 ft. It was repeatedly noticed that whatever the height of *Quercus* (up to 40 ft.), any *Arbutus* growing with it in woodland

always had its foliage sticking out from the general canopy. Its foliage, however, is very poor and straggly and the trees gradually die, being, in fact, shaded out by the more robust and wide-spreading *Quercus*. The woodland containing large trees of *Arbutus* at the present day, would seem to be the last stages of the succession leading to oak woodland, a succession which may well have started 200–300 years ago.

On the sandstone cliffs and outcrops of the Long Range and Upper Lake

In the neighbourhood of the Long Range and Upper Lake the main areas of woodland and scrub are on the lower mountain slopes. Between them and the river and lake is a varying width of flat alluvial marshland dominated by *Molinia caerulea*. On the northern side woodland extends to the lake-shore here and there along rocky river-valleys; on the southern side there are small patches of woodland on rocky headlands and large outcrops well above the level of the marsh. In nearly all such places the woodland is a *Quercus-Ilex* association (in only one place was *Rhododendron* prominent in the shrub-layer), with *Betula* and

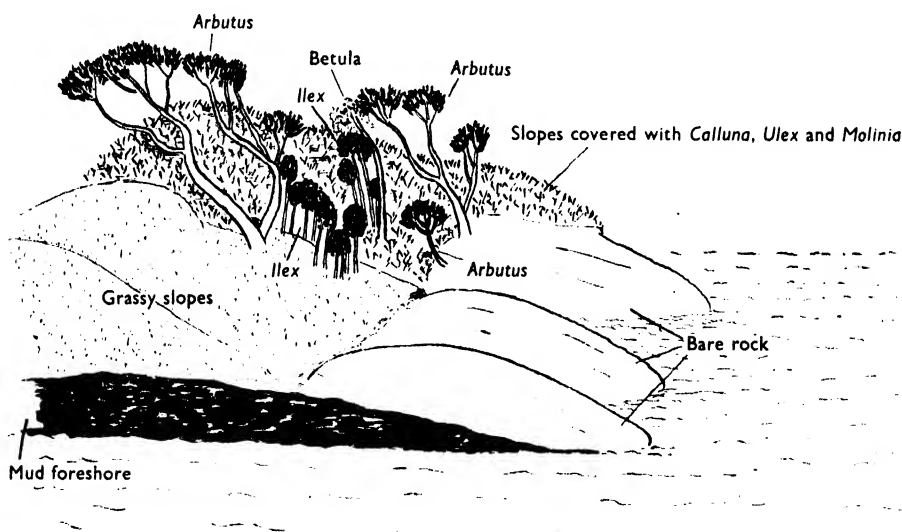


Fig. 2. Sketch of a typical rock-outcrop on the shore of the Long Range.

Arbutus as marginal plants. The *Arbutus* individuals are generally 15–30 ft. high, but the larger plants are often semi-procumbent in the lower part. One of the 30 ft. plants had a trunk 3 ft. 4 in. in girth and 6 ft. 9 in. long before branching. In one locality the woodland was mixed, and consisted of tall *Arbutus*, *Betula*, *Sorbus aucuparia* and *Quercus*, with *Ilex* forming the shrub-layer.

Throughout the marshland there are many small outcrops which take the form of low rounded ridges or small knolls (Pl. 9, photos. 1, 2). These, like the cliffs along the river and round the lake, support a characteristic open scrub of *Arbutus*, *Ilex* and *Betula*, usually accompanied by *Calluna* and *Ulex*, and sometimes with scrubby *Quercus* as well. On some outcrops the taller plants are absent, and the vegetation is principally *Calluna* (often 3–4 ft. high) with *Ulex* and *Pteridium*. On others the scrub is denser, with *Quercus* more important and occasionally dominant. But for the most part the open community is the characteristic vegetation of the outcrops (Fig. 2) as it is of the cliffs. Some of the higher

cliffs support a more luxuriant vegetation with trees of *Arbutus*, *Betula*, *Sorbus* and sometimes *Quercus*, 20–30 ft. high. In one place *Taxus* was present, which was noteworthy because it is a very uncommon plant in this sandstone area, in contrast to its abundance on the limestone. Where the more luxuriant vegetation occurred, *Arbutus* was often noted as being the tallest tree.

It is evident that *Arbutus* is as successful in the scrub and shrub communities on the sandstone as it is in similar types of vegetation on the limestone—the principal differences being that whereas *Taxus* is common and *Betula* rare on limestone, *Betula* is common and *Taxus* rare on sandstone. *Arbutus* is equally common on both substrata; its seedlings seem to be about as numerous on one as on the other, and though not plentiful they can usually be found fairly easily.

On mountain slopes

On the lower, sheltered slopes of the mountains round the Killarney lakes there are extensive areas of woodland, and, in addition, a considerable amount of scrub. Much of the woodland, whose upper limit is from 600 to 800 ft., is believed to be natural (Praeger 1934, p. 322). A great deal is climax *Quercus-Ilex* association (e.g. on the north-eastern slopes of Tomies and Shehy Mountains, and on Cromaglan Mountain), and with this *Arbutus* is normally only associated as a marginal plant. Everywhere on cliffs and steep broken rocky slopes, and above the woodland in sheltered valleys, gullies and on ledges, the woody vegetation is reduced to a scrub of *Arbutus*, *Ilex*, *Betula* and *Quercus*, sometimes with *Sorbus* as well. In addition, there are various intermediate types of vegetation between the climax woodland on the one hand, and the scrub on the other. Some of these may represent succession stages towards, or degeneration from, the climax *Quercus-Ilex* woodland, and usually *Arbutus* is one of their constituent species.

The northern side of Eagle's Nest provides an example of the conditions commonly met with. The mountain-side is steep and rocky with much cliff; the lower part is covered by open woodland of *Quercus*, *Ilex*, *Betula*, *Sorbus* and *Arbutus*, but this is replaced upwards, in gullies, under cliffs, and on ledges, by scrub of the same species. Except on ledges and in sheltered gullies, the scrub is very open with the plants widely spaced.

The northern side of Cromaglan Mountain consists of a series of cliffs and is well clad with shrubs which are crowded on the ledges and broken slopes. The principal species are *Arbutus*, *Betula* and *Ilex*, with *Calluna* and *Ulex*, and of these *Arbutus* seems to be represented by more plants than the others and extends high up the mountain-side.

Farther west the lowermost slopes of the same mountain are particularly rocky and broken, and the vegetation is almost wholly of shrubby *Arbutus* and *Ilex* with low *Betula*, *Calluna*, *Pteridium* and *Ulex*, the only trees being two tall *Fraxinus excelsa* and two *Quercus* about 20 ft. high.

Though in some places the woodland passes into scrub at its upper limit, in other places scrub is found in dry gullies and under cliffs considerably above the upper limit of the woodland and separated from it by an appreciable width of moorland. In such places single old trees of *Arbutus* are sometimes found; one example was 31 ft. long and had a trunk 4 ft. 4 in. in girth and 6 ft. long before dividing into two limbs, while another was 27 ft. long and divided from the base into two trunks each 3 ft. in girth in the lower part. These trees were nearly always more or less decumbent, and evidently dying. In one place on Cromaglan a small area of *Betula-Ilex* scrub with four *Arbutus* plants was seen on the

exposed boulder-strewn slope well above the woodland, the ground cover being *Pteridium*, *Ulex* and grasses, a sure sign that the ground was drier than the surrounding areas covered by moorland (Pl. 10, phot. 3).

The upper limit of the woodland on mountain-sides is often very uniform, the woodland ending very abruptly and not petering out into scrub. This is particularly well seen on Cromaglan, and the factor responsible would seem to be the degree of shelter, for on this same mountain the woodland was found to extend higher and to degenerate into scrub along the valleys of streams. To take an actual example, the conditions were as follows. In its lower course the stream flows through the climax *Quercus-Ilex* association, in which

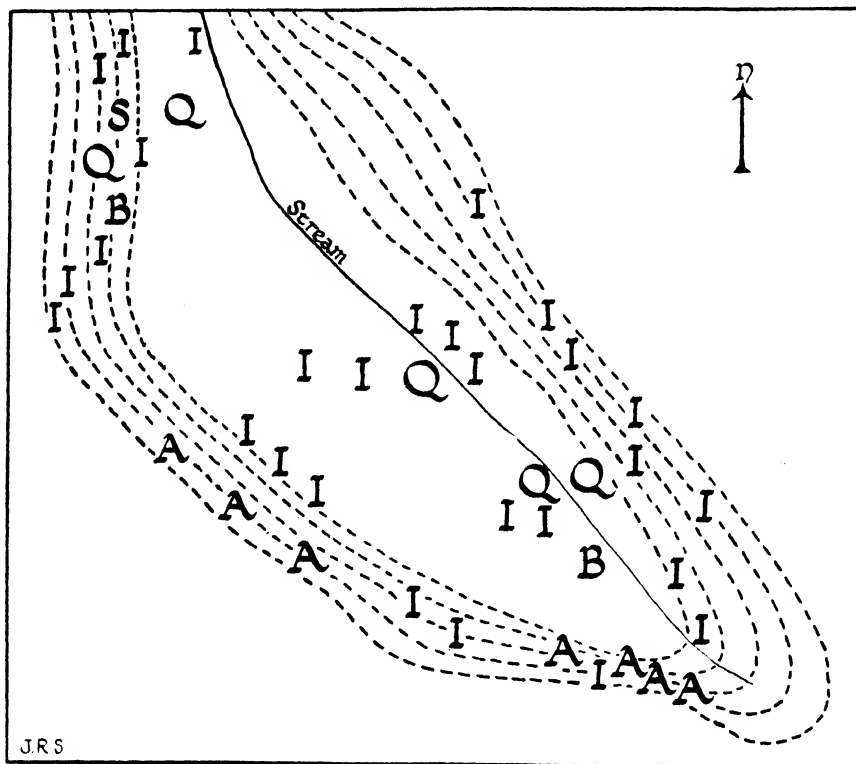


Fig. 3. Sketch-plan showing the disposition of the shrubs and small trees at the head of a valley on Cromaglan Mountain, altitude over 800 ft., high above the general level of woodland on the mountain. A, *Arbutus unedo*; B, *Betula pubescens*; I, *Ilex aquifolium*; Q, *Quercus petraea*; S, *Sorbus aucuparia*.

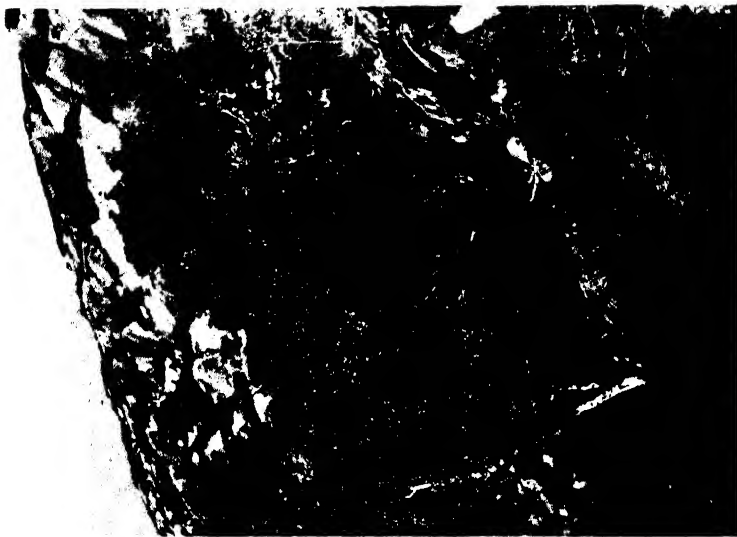
no *Arbutus* was seen. Above the general upper limit of the woodland the stream flows in a deep valley with rocky sides, and woodland continues in the bottom of the valley—*Arbutus* being present on the very rocky banks of the stream itself, associated with *Quercus*, *Ilex* and *Sorbus*, the trees being up to 30 ft. high. On the valley sides above this mixed woodland there is a scrub of *Arbutus*, *Betula*, *Taxus* and *Ilex*, while towards the head of the valley, which was fairly broad and enclosed by broken cliffs, the woody vegetation was largely *Ilex* scrub, with a few plants of *Arbutus*, *Quercus*, *Betula* and *Sorbus* (Fig. 3; Pl. 10, phot. 4; Pl. 11, phot. 6). The head of this valley (as of others where similar conditions are found) is between 800 and 900 ft., and thus considerably above the general level of the woodland which is here about 700 ft.



Phot. 1. Characteristic rounded rock-outcrops in the *Molinia* marsh, south side of the Upper Lake.



Phot. 2. Part of one of the outcrops shown in Phot. 1; *Betula pubescens* on the extreme left, then *Arbutus unedo*, to the right of which is a close group of plants of *Ilex aquifolium*.



Phot. 4. Plants of *Arbutus unedo* at the head of the valley (see Fig. 3) of a stream on Cronaglan Mountain, altitude over 800 ft., high above the general level of the woodland.



Phot. 3. Isolated plants of *Arbutus unedo* on Cronaglan Mountain at about 800 ft., well above the level of the woodland, and separated from it by a wide stretch of moorland.



Phot. 5. Small trees of *Arbutus unedo* round the margin of a rocky headland on the south shore of Lough Leane.



Phot. 6. Plants of *Arbutus unedo* in another part of the valley-head shown in Phot. 4 and Fig. 3.

In conclusion one exceptional instance of the occurrence of *Arbutus* right inside climax *Quercus-Ilex* woodland may be mentioned. In this place two rocky knolls, one 40 ft. long and 20 ft. high, the other smaller, broke the comparative regularity of the mountain-side. Across the top of the larger knoll lay an *Arbutus* 30 ft. long, at one end were four plants of *Arbutus*, 9–15 ft. high, and elsewhere there were several plants of *Ilex*, one small *Sorbus* and a stunted *Quercus* 15 ft. high. On the second knoll were four plants of *Ilex*, two *Arbutus* plants (one 20 ft., the other 9 ft. 6 in. high), two small *Sorbus* and plants of *Calluna*, *Vaccinium myrtillus*, *Saxifraga spathularis*, *Lonicera* and *Rubus fruticosus*. These rocky outcrops had, one might say, permitted the development of islands of scrub within the otherwise climax woodland.

Swollen stem-base and regeneration

Plants of *Arbutus unedo* are extremely tenacious of life. In old age plants growing in exposed places commonly become decumbent, only the leafy twigs at the extremity of the tree growing upwards, but the trees remain firmly anchored in the clefts of rock in which they grow. Also it is not unusual to see, in an open situation, an old tree with a new growth, having the appearance of a young plant, in the basal part of the trunk, the tree itself being more or less prostrate and apparently dead. Furthermore, plants survive damage to the main stem, whether accidental or intentional (as by coppicing), sending up new shoots from the base to replace the damaged stem. There is, however, no true vegetative reproduction, for example, by suckers, and regeneration from seeds is therefore essential for the maintenance of the species as part of the natural flora. The tenacity of life of individual plants may be related to the fact that early in their existence plants of *A. unedo* develop numerous adventitious buds in the lowermost part of the stem (which is well below ground-level), these buds being associated with considerable proliferation of the tissues of the stem in their vicinity, so that this part of the stem becomes noticeably enlarged. An account of this swollen stem-base has already been given (Sealy, 1949). It appears to be a normal feature in the species, since it was present in all the nine young plants collected at Killarney (Fig. 4) and in ten of the eleven young plants grown at Kew. One of the latter was examined when it was 4 years old, and has been described in detail (Sealy, 1949, pp. 243–5); three more were dug up after being killed during the severe winter of 1946–7; while examination of the remaining seven, living, plants, now (1949) in their twelfth year, showed that six had either a conspicuous unilateral swelling or the base of the stem much enlarged, while the seventh plant showed only a slight indication of irregularity. The swollen part of the stem is evidently comparable with a similar structure found in *A. menziesii* and in other genera, for example *Arctostaphylos* and *Eucalyptus*. In *Arbutus unedo* it starts as a small swelling in the region of the cotyledons and increases in size as the plant grows larger, the degree of development apparently depending on the condition of the plant. The structure can scarcely be essential for the growth of the plant, but its presence may be advantageous in three ways. First, it provides a reserve of buds from which new shoots can be developed should the original stem become damaged (see Fig. 4D, E). Secondly, it may serve as a storage organ, for aleurone grains are plentiful in the swollen region as they are in *A. menziesii*. Thirdly, it helps to hold the plant firmly in the clefts and fissures of the rock in which it grows. All the young plants collected at Killarney all proved difficult to uproot, and the older plants were never uprooted. In *A. menziesii*,

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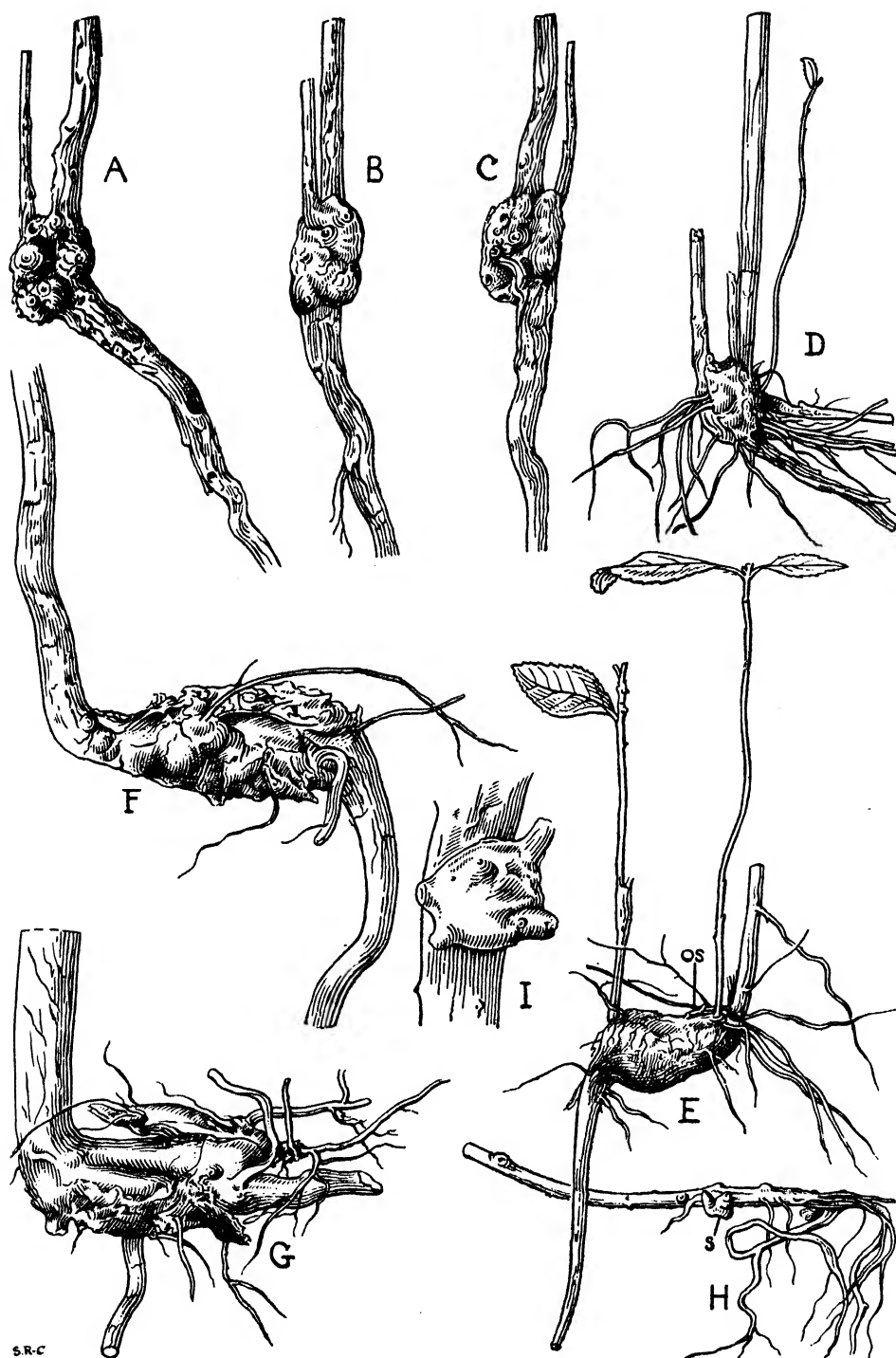


Fig. 4.

Arctostaphylos species, and *Adenostoma fasciculatum*, emphasis has been laid on the value of the swollen stem-base in regeneration after fire (Jepson, 1916, 1936, 1939*a, b*). These plants belong to the Californian plant-communities known as 'chaparral', which are the equivalent of the Mediterranean 'macchia' in which *Arbutus unedo* often plays a prominent part, being for the most part evergreen shrub-communities developed under similar climatic conditions. It is therefore possible that the swollen stem-base has a similar biological significance in all the plants in which it is found, and that it is related to the habitat, though not necessarily to the incidence of fire.

As already mentioned, regeneration from seeds is essential for the maintenance of *A. unedo* as part of the natural flora. This appears to be accomplished satisfactorily at Killarney, where seedlings of all ages from those of the current year upwards were observed and examples collected. Though the young plants were numerous enough to maintain the species, they were not abundant, and their number can be no relation to the enormous number of seeds produced during a normal year. In both years when visits were made to Killarney (1935 and 1938) the abundance of fruits was particularly noticeable. This, we were told, was normal. The crop was equally good in 1936, so Mr Denis J. Doody, of the Muckross Gardens, informed me, while 1937 was described by him as 'a wonderful year for berries of all kinds'. Thus for the four consecutive years 1935-8 the crop was heavy. It was, however, extremely poor in 1947 according to Dr D. A. Webb, no doubt as a result of the exceptionally severe winter of 1946-7. It would seem that normally the crop is heavy; the number of fruits is beyond computation, and since each contains twenty to thirty seeds, the number of the latter must be astronomical. The fruits are greedily eaten by birds (at Kew mainly by blackbirds and thrushes, while at Killarney great flocks of wood-pigeons are said to clear the trees) and the seeds are distributed in castings and droppings. Many fruits escape being eaten and fall to the ground, and it was demonstrated experimentally at Kew that seeds will germinate from whole fruits whether the latter are covered or not. The small number of young plants at Killarney compared with the immense output of seeds indicates a tremendous wastage. As *A. unedo* is primarily a plant of open rocky situations, much of the wastage must be due to dispersal to unsuitable habitats, but other factors, namely seed viability, conditions governing germination, and seedling mortality, have also to be considered.

Legend to Fig. 4.

Fig. 4. The swollen stem-base in young plants of *Arbutus unedo* from Killarney. A-C, three views of the base of a plant (no. 400) 20.5 cm. high, with the swollen part 2 cm. long and 1.5-2 cm. in diameter; D, from a plant (no. 940 D¹) whose original stem, on left, had been broken and replaced by a new shoot (centre) 22 cm. high which, like the weak shoot (right), had arisen from the swollen region, this being 1.5 cm. long and in diameter; E, from a plant (no. 940 D²) whose original stem (os) had died off, the present stem, on right, had been damaged and was only just over 10 cm. high, and, like the two weak shoots, it had arisen from the swollen part which was 2 cm. long and 1.5 cm. in diameter; F, from a plant (no. 402) 50 cm. high with the swollen part 5 cm. long and 2-2.7 cm. in diameter; G, from a plant (no. 403) 67 cm. high with the swollen region 4.5 cm. long and 1.5-2 cm. in diameter; H, basal part of a 5-year-old plant (no. 940 C) 17 cm. high, with a small swelling (s) 5-6 mm. across; I, swelling from H, $\times 4$; all other figures two-thirds natural size. In addition three other plants were collected, namely: no. 940 B, 13 cm. high with a small swelling like that of 940 C shown above; no. 401, 28 cm. high with the swollen part 2.5 cm. long and 1.5-1.9 cm. in diameter; and no. 940 E, about 45 cm. high with the swollen part 4.5 cm. long and 2.5 cm. in diameter.

Germination experiments and the growth of plants

In order to obtain data on seed viability, germination, and seedling mortality, ripe fruits of *A. unedo* were obtained from Killarney in 1937, and a number of cultures were set up at Kew. Only one set of experiments was made, and the results cannot therefore be used as precise indications of the effect of the various factors tested. There were, however, sufficient cultures (eighteen using fifty seeds each, and three using twelve fruits each) to provide ample scope for observations on germination and growth of the seedlings, and also to permit general conclusions to be drawn about other features.

Seeds washed free from the pulpy matrix of the fruit, and also whole fruits, were sown in pans in different media and under different conditions—i.e. some were left exposed on the surface of the medium, others were covered; some were in full light, others were partially shaded; some seeds were scarified, others were not. All the experiments were in an unheated greenhouse from October 1937 until June 1938, when they were all taken outside. They remained out-of-doors until October 1938, when most of them were again placed in the greenhouse. The first sign of germination (of which I have given a brief account elsewhere, Sealy & Webb, 1949) was seen on 19 January 1938; optimum germination was reached by 5 February in cultures where the seeds were left exposed, but not until a month later where seeds were covered. Seeds germinated quite well from whole fruits, whether covered or not. Although the cultures were not disturbed for over 12 months, no seeds germinated after 5 March 1938, so that the germination period was quite short, 14–19 weeks from the time of sowing. Viability was of the order of 42–68%. Seedling mortality—almost entirely confined to the first 3 months—was about 60% for seeds and fruits sown in full light (eighty-nine survivors from 220 germinations), and 100% for seeds and fruits in shade (no survivors from fifty-four germinations). Shading had little effect on percentage germination, but proved lethal to growing seedlings. Incidentally, no plant of *A. unedo* was seen growing in shade at Killarney—this was a point to which particular attention was paid during field work. Scarification of the testa had no noticeable effect on germination, nor, within the limits tested, had the pH value of the medium, germination and growth being about equal in all values from pH 4 to 6.5. The exposure or covering of the seeds and fruits did not have any marked effect on the numbers of seedlings established, but the texture of the medium did seem important in this respect, and the best results were obtained by scattering the seeds on a thick layer of sphagnum moss over peat. Owing to the loose texture of the moss the seeds were washed down some 3–4 cm., and in that position were both moist and well aerated. Twenty-eight out of the fifty seeds germinated, and all the seedlings became established and grew very well. It was noticeable that on germination the radicle was able to grow straight through the moss and pierce the surface of the peat without difficulty, while the cotyledons were easily unfolded and pushed out from the moss. Until they grew large enough to feel the effect of the restricted root-room, these seedlings were quite the most robust and healthy. Next to sphagnum moss and peat, humus proved the best medium for seedling establishment, no doubt on account of its relatively loose texture. The different media, peat, humus and limestone, and garden soil, had no perceptible effect on the amount of growth once the seedlings were established. Seedlings could not withstand drought, and those allowed to become dry died very quickly. Excessive moisture at the root was likewise fatal, and eight vigorous seedlings were dead by the end of 3 months during which the medium (peat) was kept waterlogged. Five

1-year-old plants passed the winter of 1938-9 out-of-doors without ill effect, but the following severe winter was disastrous to the 2-year-old plants that were left unprotected—sixty-four being killed out of eighty-five, with nine others killed back to the basal 1-2 cm. of stem, leaving only twelve undamaged. Of the five plants that had passed the previous winter out-of-doors, two were killed and three were unharmed.

Seedlings 4-5 cm. high have leaves 15 mm. long and 8 mm. wide, succeeding leaves becoming progressively larger. The amount of growth made depends almost entirely on the amount of room available to the plant. Where root-room is restricted, whether by the nature of the situation in which the plant is growing or because numerous seedlings are crowded together, seedlings may be only 2-7 cm. high at the end of the first season's growth. In better conditions they attain 8-13.5 cm. in the same period, while one plant reached a height of 17 cm. Grown on a second season under the same conditions, the restricted plants became 5-23 cm. high, while those in better conditions attained 28-44 cm. The effect of the conditions in the early stages of the plant's growth influences its development for many years. Thus of eight 10-year-old plants which had been planted out in the same plot of ground for the last 6 years, two were 2 ft. 6 in., one 4 ft., two 4 ft. 6 in., two 5 ft., and one 6 ft., in height, the differences in size corresponding to the unequal development of the early years.

At Kew, plants of *A. unedo* gradually pass into a resting state in October. The leaves remain green unless damaged by cold, but no fresh leaves appear, nor do the youngest existing leaves increase in size, and the plants pass the winter in the condition they had reached in October. Plants in a cold greenhouse begin to grow again in mid-February, and new leaves are developed by mid-March. Out-of-doors at Kew (and also, apparently, at Killarney) growth is usually resumed about the first week of April. The plants grow vigorously throughout the spring and summer, but during September vegetative growth slows down and by the end of October it has come to a standstill. In September the first flowers open on older plants and 'flowering' continues until December. A few inflorescences were formed on the largest seedling plants at Kew for the first time when they were 8 years old; the flowers opened but no fruits were formed. On older plants at Kew fruits are normally few, in contrast with the conditions at Killarney, where, as already mentioned, the trees usually fruit abundantly. The fruits develop slowly throughout the ensuing 12 months, and are ripe the following October-November, when the trees are again in flower.

Conclusions

At Killarney *A. unedo* is primarily a plant of such habitats as cliffs, broken rocky slopes, and rock outcrops, which are edaphically unsuitable for woodland, and where the vegetation is limited to shrub communities or scrub. In these habitats the species is extremely successful and maintains itself with ease by regeneration from seeds. It flourishes equally well on Carboniferous Limestone and on Old Red Sandstone, in 'soils' with pH values of 4.4-5 to 6.5-7. On the limestone its principal associates are *Taxus baccata* and *Ilex aquifolium*, but *Sorbus aucuparia*, *Corylus avellana*, *Betula pubescens*, *Quercus petraea* and *Sorbus rupicola* may also be represented. On the sandstone *Arbutus* is most frequently accompanied by *Ilex* and *Betula*, less often by *Sorbus aucuparia* and *Quercus*, and rarely by *Taxus*. *Arbutus* is also a marginal plant of oakwoods, and sometimes forms part of the woodland in the succession stages leading to climax oakwood. It cannot endure shading, and when growing in company with *Quercus* will reach a height of 40 ft. in competition for

light. Owing to its poor canopy it cannot compete successfully with *Quercus*, and is eventually shaded out. *Arbutus* also reaches tree size when a number of plants grow together in a close stand, but this probably only happens when the group of *Arbutus* plants becomes surrounded by *Quercus*.

At Killarney an immense number of seeds is normally produced each year, but the number of seedlings is very small in comparison with the seed output. This is probably due primarily to dispersal of the seeds to unsuitable habitats. Then, since seed viability would seem to be of the order of 55%, not more than half of the seeds which reach favourable sites may be expected to germinate. Finally, seedling mortality can be expected to reduce the number of plants to a third or less, since loss of seedlings in the wild is likely to be in excess of the 60% recorded under experimental conditions. It is impossible to estimate the minimum seed output necessary to maintain *A. unedo* in its natural habitats, but taking into account the fewness of the young plants at Killarney relative to the immense seed production, and the fact that there is still plenty of room available for more plants, it seems safe to say that a very heavy output of seeds is necessary to overcome the hazards of dispersal to suitable habitats, seed viability and seedling mortality. This would be in agreement with Salisbury's conclusions that plants of intermittently available habitats and those of open habitats are generally characterized by at least moderately heavy seed production (Salisbury, 1942).

Finally, it may be noted that the occurrence of *A. unedo* as a member of shrub- or scrub-communities on cliffs, rocky slopes, etc. at Killarney, is in keeping with its behaviour in the Mediterranean region, where it forms an important constituent of the shrub-communities known as 'macchia' which are commonly developed on steep rocky hillsides, on cliffs, and in the limestone karst regions.

THE DISTRIBUTION OF *ARBUTUS UNEDO*

Distribution in general

The genus *Arbutus* L. comprises some twelve to twenty species. Four are natives of the Old World, while the remainder, whose number remains uncertain pending taxonomic revision, are indigenous to North America.

The Old World species are essentially Mediterranean plants. Two are of restricted distribution—*A. canariensis* Duhamel confined to the Canary Islands, and *A. pavarii* Pampanini known only from a small area in Cyrenaica—while the other two are widely distributed, *A. andrachne* L. being found over much of the eastern Mediterranean basin, and *A. unedo* L. ranging throughout all the lands of the Mediterranean basin except Libya and Egypt (Fig. 5).

A. unedo is a typical 'Mediterranean' plant, a tough-leaved evergreen shrub or small tree, and is one of the chief constituents of the Mediterranean shrub communities known as 'macchia' or 'maquis'.* The hot dry summers characteristic of the region are inimical to plant growth, and in *Arbutus*, as in other evergreens, growth comes virtually to a standstill during the summer. The flowering period is late September to December, and fruits are ripe twelve months later, when the plants again come into flower. Vegetative growth is

* For descriptions and constituent species of the various types of 'macchia' see Béguinot (1901, 1912), Bergen (1903), Daveau (1906), Knoche (1922-3), Raunkiaer (1916, 1934), and Turrill (1929, 1937).

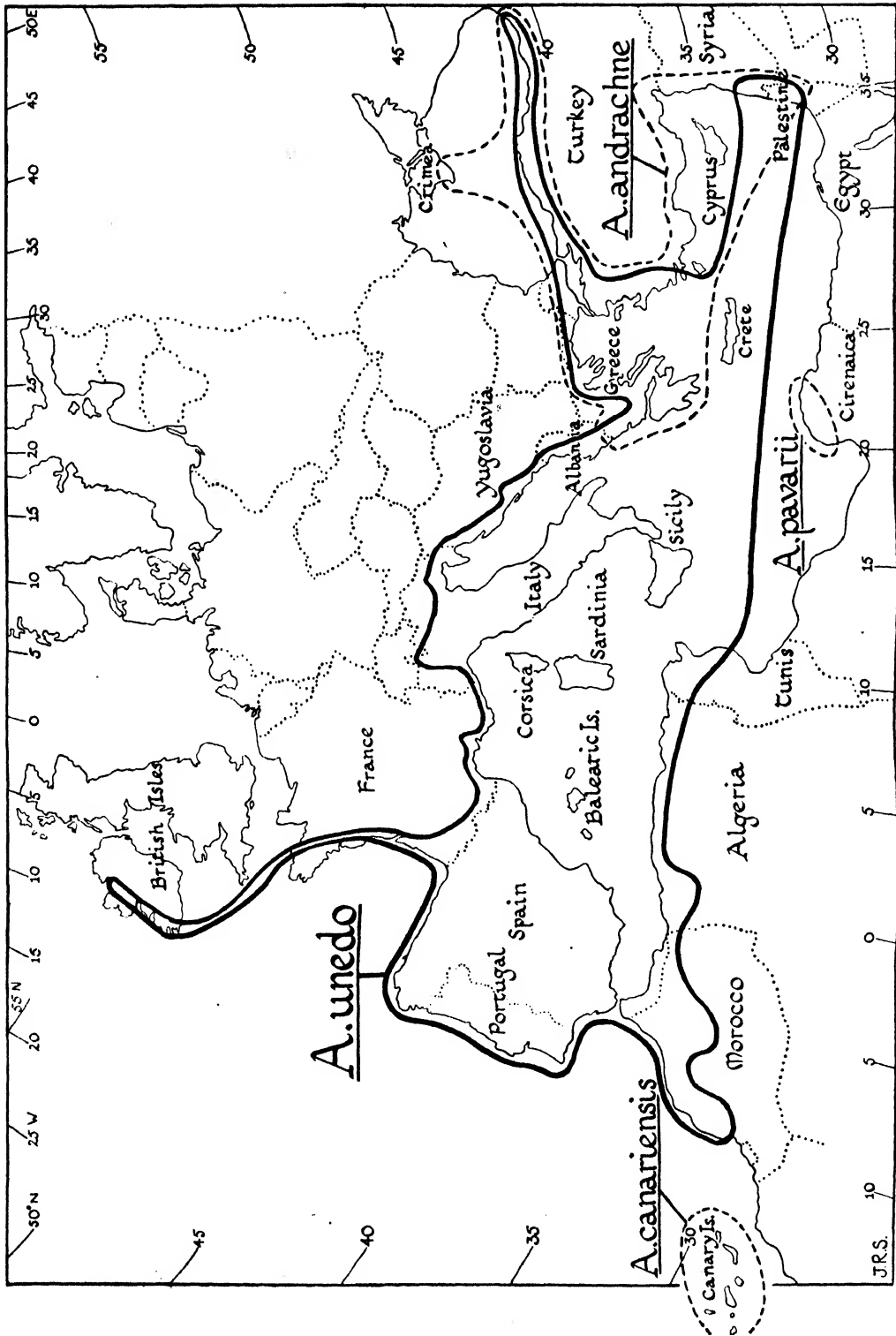


Fig. 5. Map showing the distribution of the Old World species of *Arbutus*.

resumed after the flowering, continues through the spring, and gradually slows down as summer advances.

The species is not confined to the Mediterranean region, for it is found throughout the Iberian Peninsula and also in the south-western littoral of France, where it occurs as far north as La Rochelle. It is also found much farther north, in three isolated localities, namely: (1) in Brittany, on the cliffs of Trieux near Paimpol; (2) in south-west Ireland, chiefly around the lakes of Killarney but with discontinuous extensions south-westwards to Lough Currane and south to Adrigole and Glengarriff; (3) in north-west Ireland around Lough Gill, Sligo, which is about 160 miles north of Killarney.

Throughout much of its distribution in the Iberian Peninsula, the species grows under climatic conditions similar to those of the Mediterranean region. In the northern and north-western areas, however, the summers are cooler and there is rain at all seasons. Similarly, in the Landes of south-west France the summers, though warmer than in northern Spain, are not dry, the rainfall in the driest months being more than half of that in the wettest months. In all these areas the summer is not, therefore, a season unfavourable for plant growth, as it is in the Mediterranean region, though during the rest of the year the climatic conditions agree with those of that region. Phytogeographically northern Spain and south-west France could be regarded as modified extensions of the Mediterranean region—the modification being the absence of the summer resting period. For an evergreen like the *Arbutus* this simply means that conditions are suitable for growth throughout the year, and presumably there is no resting period.

In Brittany and Ireland, however, the *Arbutus* is in a very different phytogeographical region, where the winter is definitely a period unfavourable for plant growth. In this region *A. unedo* passes the winter in a dormant state; vegetative growth comes to a standstill in October, and is resumed about the beginning of the following April; it continues throughout the spring and summer, and gradually slows down in the autumn. The vegetative resting period is therefore different to that in the Mediterranean region, though the flowering and fruiting periods are the same. In north-west Europe the total growing period is April to November–December (when winter weather conditions put an end to flowering), whereas in the Mediterranean region it is October to June or July (when summer heat and drought brings vegetative growth to a standstill). The adaptability of the species, so far as the growing and resting periods are concerned, is obviously due to its evergreen nature, but it is interesting that the flowering period remains fixed. The flowering in north-west Europe might have been expected to be delayed until after the resting period to be in agreement with the condition in the Mediterranean region.

From the published accounts (Avice, 1896; Praeger, 1932*a*) it appears that in Brittany and at Sligo *A. unedo* grows under much the same general conditions as at Killarney, that is, it forms part of shrub-communities on broken rocky ground, cliffs, etc. (which is, of course, in keeping with its behaviour in the Mediterranean region), it maintains itself in competition with other members of the flora, and gives every appearance of being native. The plants growing in north-west Europe are taxonomically identical with those of the Mediterranean region. Comparison of extensive collections made at Killarney with those from the Mediterranean preserved in the Kew Herbarium showed that the plants agreed perfectly in all morphological and anatomical details. The variation in leaf-size and shape—which is very considerable—was almost the same in the material from the two regions. The species is evidently able to grow as well in north-west Europe as in the Mediterranean

region, and the question arises 'why should it occur in north-west Europe only in three widely separated localities?' The factors involved in the success of any species as a member of a natural flora may be summarized as: (1) the climatic conditions must be within its degree of tolerance; (2) the substratum must be suitable; and (3) there must be no undue limitations imposed by biotic factors such as competition, diseases, pests, etc. These factors in combination must be such that the individual plants can survive, and adequate regeneration is possible. In seeking to explain the discontinuous distribution of *A. unedo* in northern Europe, the obvious first step is to find out if any of the factors mentioned above, or any combination of those factors, limits the species to the three stations it occupies. This may be conveniently considered under the two headings of Survival of the Individuals, and Regeneration.

Conditions for survival in north-west Europe

(a) Climatic conditions

The three northern localities for *A. unedo* are all in the mildest part of north-west Europe, in the zone with a mean actual January temperature of 40° F. (Fig. 6). In this zone the winters are mild, there is little or no frost save in exceptional years, and even then it does not last long. In its Mediterranean stations the species is found in climatic conditions which vary considerably from place to place, but which agree in the summers being hot and sunny, the winters mild, and the rainfall occurring in the winter half of the year. The amount of rainfall varies greatly, from 52 in. at Genoa and 48 in. at Corfu to 20 in. at Seville and 15.5 in. at Athens.* The climatic conditions likely to limit the occurrence of *A. unedo* in north-west Europe are, therefore, winter cold and lack of summer sunshine. The fact that the species grows well at Killarney where there is much cloud and the total hours of sunshine is relatively low (Valencia, about 30 miles west of Killarney, has 1442 hours per year—compare Rome 2362 hours and Athens 2655 hours) indicates a wide degree of toleration in this respect. It follows that only winter temperature has to be considered as a possible limiting factor. The species actually grows quite well under colder conditions than those of its natural habitats, for example at Kew where the mean actual temperature for January is 38.9° F. In these colder areas, however, there is some risk that plants may be damaged, or even killed, during exceptionally severe winters (Bowles, 1919; R.H.S., 1948). During the severe weather of 1939–40 a number of large shrubs of *A. unedo* were killed at Kew, as were sixty-four out of eighty-five 2-year-old seedlings, nine of the remainder being killed back to the base. Similarly, in the hard winter of 1946–7, out of ten 9-year-old plants growing at Kew two were killed (one was about 4 ft. high, the other almost 6 ft.), two others (one about 2 ft., the other over 6 ft.) were killed back to the hard wood, and though they produced small shoots during 1947 they died the following year, while the remaining six plants were all more or less severely damaged. These ten plants were all vigorous bushy shrubs, the differences in size being due to the different treatment accorded to them during their first 4 years. They were growing in line and just touching one another. The largest, which was killed back to the hard wood and eventually succumbed, was at one end of the line and close to a wall, in what was thought to be the most sheltered position. The other three specimens that were killed were all in intermediate positions.

It seems probable that the species cannot tolerate much colder conditions than those of

* These and other climatic data are taken from Kendrew, *The Climates of the Continents*, ed. 3 (1937).

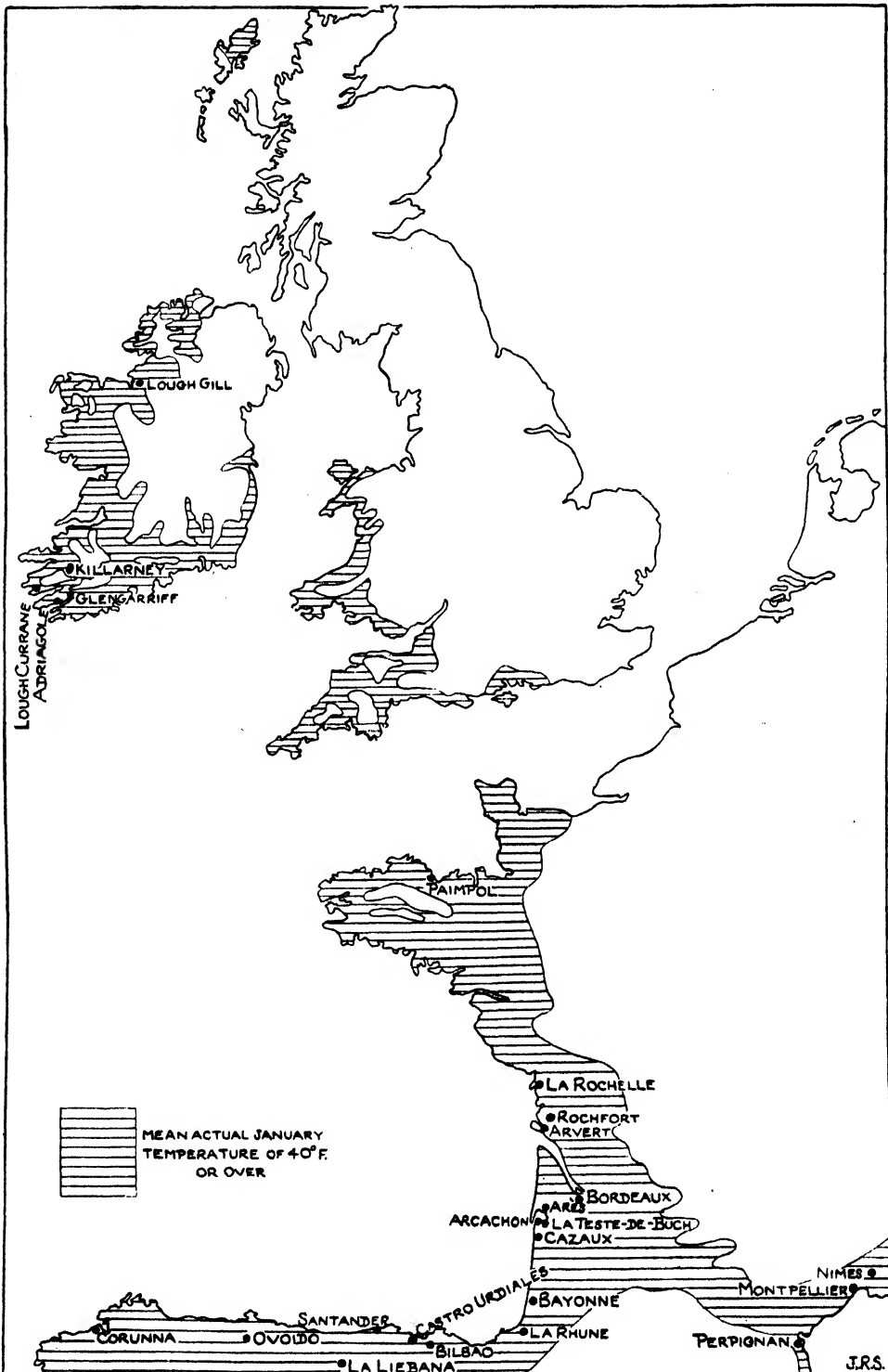


Fig. 6. Map of the British Isles, western France, and northern Spain, showing the area with a mean actual January temperature of 40° F. or more (shaded), and the localities from which *Arbutus unedo* has been recorded.

the London area, and hence winter cold would limit its distribution in northern Europe to areas with a mean actual January temperature above 38° F.

(b) *Substratum conditions*

At Killarney *A. unedo* thrives equally well on Carboniferous Limestone and on Old Red Sandstone. In cultivation it grows satisfactorily under a very wide range of soil conditions, with the pH value varying from 4 to 7. It requires good drainage, however, and cannot tolerate a waterlogged soil. At Killarney the natural habitats are open rocky places such as cliffs, broken rocky slopes, etc., where it grows in fissures of the rock. It seems that provided drainage is good *A. unedo* is tolerant of a wide range of substrata.

(c) *Biotic conditions*

A. unedo is singularly free from diseases and pests, and there is no record of anything of this nature limiting its occurrence. In north-west Europe its range might well be restricted, at least to some extent, by human activities, and in this respect the mention of *Arbutus* in the Brehon Laws as one of the plants interference with which constituted trespass (Praeger, 1934, p. 129) may not be without significance. Avice (1896) says that cart-loads of branches were cut each year from the trees in the Brittany locality, for use as decoration on the feast-day of the patron saint of the neighbouring town, and that the plants also provided fuel for the farmer who owned the land upon which they were growing. It is also known that in by-gone times *Arbutus* was used in Ireland as a source of charcoal for smelting the silver, lead, and copper ores mined in the Killarney area. Another biotic factor likely to limit the distribution of *A. unedo* in north-west Europe is competition with *Quercus petraea*. As already described, the *Arbutus* grows at Killarney primarily as a constituent of shrub-communities or of scrub. It also occurs as a marginal plant of woodland. It is intolerant of shading, and never forms part of the shrub-layer in woodland as *Ilex aquifolium* does. Consequently, when growing in close stands or in competition with *Quercus*, *Arbutus* plants will grow up into trees 30–40 ft. high. As a member of the tree-layer *Arbutus* cannot compete successfully with *Quercus* and is always eventually shaded out. The survival of the species as part of the natural flora therefore depends on the presence of habitats where the vegetation is limited to shrub-communities or to scrub, conditions under which *Arbutus* can compete successfully with other plants.

Regeneration in north-west Europe

As already described (p. 375) *A. unedo* is noteworthy for its immense seed production. This would appear to be necessary at Killarney to ensure its success as a member of the native flora in view of its specialized, and often intermittently available, habitats. This would also, presumably, be true for other localities in north-west Europe. In this connexion attention must be drawn to the fact that in colder climates, such as that of Kew, production of fruits by *A. unedo* is extremely meagre. Normally, the trees bear very few fruits, and only once in the last 50 years have they borne a crop comparable with those at Killarney; the exception was in 1935, and was almost certainly due to the fact that fine warm weather continued well into the autumn of 1934, which meant that bees and other insects were still flying when the *Arbutus* was in flower and pollination was possible on a large scale. Since the flowering period is September to December, the paucity of fruits

at Kew in normal years is probably due primarily to the lack of pollinating agents during the flowering period. There is also the fact that flowers at Kew are not infrequently damaged by bad weather, especially by fogs and severe frosts, while the very young fruits are also liable to be damaged by hard weather. It seems safe to conclude that the output of seeds at Kew would be insufficient to enable the species to maintain itself in nature. It follows that in regions with winters less mild than those of its present stations, *A. unedo* would be unable to persist as a member of the natural flora owing to its inability to regenerate. That is, the species is limited by the regeneration factor to the zone with a mean actual January temperature of 40° F. or more.

Conclusions

The zone to which *A. unedo* is limited by the regeneration factor includes much of north-west France, south-west England, south and west Wales, and southern and western Ireland—see Fig. 6. Within this zone the species could grow wherever conditions permit the development of *Quercus* woodland, and also where edaphic conditions limit the woody vegetation to shrub-communities or scrub. In point of fact *A. unedo* could never be more than a marginal plant in woodland, since it cannot compete successfully with *Quercus* as a tree, and cannot exist in the shrub-layer owing to its intolerance of shading. Its existence in north-west Europe as a member of the flora under natural conditions therefore depends on the presence, in areas climatically suitable for woodland, of habitats such as cliffs and broken and rocky slopes, where the woody vegetation is limited to shrub-communities and scrub. In such habitats, as already explained, *A. unedo* is eminently successful. Now despite the extent in north-west Europe of the zone climatically suitable for *Arbutus*, there are few localities where the ecological conditions are completely favourable, and there is probably nowhere else to compare with Killarney. In its two other northern localities, at Trieux and near Sligo, the species is much restricted and is perhaps dying out. Dr Praeger has suggested (1932*a*, p. 111), mainly on the evidence of place names, that *A. unedo* was formerly much more widely distributed in western Ireland. If this be correct then the area occupied by the species has become greatly contracted during historical times, and the process may still be continuing. To what extent this has been due to human activities it is impossible to say, but it is at least possible that man may have played some part.

When all the factors are considered, the present restriction of *A. unedo* to its three northern stations would seem to be the natural consequence of existing conditions, that is, it does not grow elsewhere in northern Europe as part of the native flora because it cannot do so.

THE ORIGIN OF *ARBUTUS UNEDO* IN IRELAND

On account of its peculiar distribution *A. unedo* is generally grouped with certain other species whose origin as part of the British flora has long been a matter for speculation and discussion. The species, all of which except one are restricted in the British Isles to western Ireland, are: *Neotinea intacta* (Link) Reichb. f., *Pinguicula grandiflora* Lam., *Daboecia cantabrica* (Huds.) C. Koch, *Erica mediterranea* L., *E. mackaiana* Bab., *Saxifraga hirsuta* L., *S. spathularis* Brot. (which is found in Wicklow, eastern Ireland, as well as in the western part of the country), and *Arbutus unedo* L. Together they constitute the so-called

'Lusitanian' element of the British flora. Apart from the fact that in the British Isles they all occur in western Ireland, they have little in common. Ecologically they differ considerably one from another, and there are also marked differences in the details of their geographical distributions. To group these diverse plants together and to seek a single explanation to account for their distributional peculiarities seems illogical. Each species presents a distinct problem and needs detailed investigation. Nevertheless, they have been associated on distributional grounds, and four theories have been put forward to account for their present distributions, namely:

- (1) That these plants are relicts of the Tertiary flora of the British Isles, and that they survived the glacial epoch in, or near, the areas where they are now found (Forbes, 1846; Praeger, 1910, 1932*b*).
- (2) That they represent accidental introductions by man in post-glacial times (Hennessey, 1867).
- (3) That they are chance introductions from seeds carried by birds in post-glacial times (Reid, 1899, 1912); Roi has recently (1937) suggested that this may be true for *Arbutus* but not for the other species.
- (4) That these plants formed part of the flora which invaded the British Isles from the continent after the retreat of the ice, and that their distributions were originally continuous, but have become broken up as climatic conditions changed during later periods (Stapf, 1912, 1914, 1917).

The second and third alternatives have been largely abandoned, mainly because of the existence of a small group of animals with distributions comparable with those of the plants. Both the other theories are supported by contemporary botanists, and it is interesting to consider their application to *A. unedo*.

Wilmott (1930) and Farrington (1932) both deduced from Simpson's theory of the cause of Ice Ages (Simpson, 1929, 1940) that a warm pluvial climate may have prevailed in ice-free areas quite near the ice-sheets during the glacial epoch. The suggestion is made that plants like *A. unedo* could have survived in the south-west of the British Isles so long as the southern parts of these Islands were ice-free. This, however, seems to overlook the fact that any such ice-free areas would be at the fringe of a great sheet of ice, which at maximum glaciation is estimated (Seward, 1931) to have covered approximately eight million square miles of the northern hemisphere, and which must have been the most important factor determining the climate of the whole northern hemisphere. Whatever the summer conditions, winters in the unglaciated areas adjacent to the ice must have been long and severe. This conclusion is supported by geological evidence,* all of which points to severe climatic conditions, not only in southern England and Ireland, but also in Brittany. It is inconceivable that *A. unedo*, which is near its limit of climatic toleration in the present climate of the London area and which needs a winter climate at least as mild as that of Killarney to maintain itself in nature, should have persisted in or near the British Isles during the whole of the Quaternary glacial period.

Du Rietz (1935) suggested that 'at least most of the oceanic flora of the British Isles survived the Pleistocene glaciations in a glacial forest region south and south-west of Ireland and England', and he cites instances of forests near glaciers at the present time in Alaska, Greenland, New Zealand and Patagonia. It is scarcely necessary to point out

* Bonney (1911, pp. 14-23), Boswell (1935), Charlesworth (1930), Hollingworth (1935), Reid (1899, pp. 39-42; 1912, pp. 574-5), Sandford (1935), Seward (1931), Woodhead (1929, pp. 5-7) and Wright (1914, 1937).

that *A. unedo* could not survive in climatic conditions such as those of Alaska and Greenland. So far as New Zealand and Patagonia are concerned, the forests are growing under climatic conditions which are not determined by, and are only slightly modified by, the presence of the ice—which is totally unlike the conditions that existed during the Pleistocene glaciations, when, as already mentioned, the immense ice-sheets must have been the principal factor determining the climate over much, if not all, of the northern hemisphere.

The recent find of fossil remains of *Rhododendron ponticum* L. in an inter-glacial deposit at Gort, Co. Galway (Jessen, 1948) is of interest when considering the effects of the later phases of the Pleistocene glaciations. According to Jessen fossil evidence shows that this species was widespread in central and southern Europe during the inter-glacial period, and the latest discovery indicates that its range extended to western Ireland. At the present time the species is distributed from the region of the Caucasus westwards through Asia Minor to southern Bulgaria, and in addition it occupies three isolated areas in south Spain and south and west Portugal which Jessen thinks are relicts of its former much more extensive range. No explanation is put forward for the remarkably drastic reduction that has taken place in the area of distribution of the species, but if this should have been due to the last glaciation, it would suggest that conditions in western Ireland were much too severe for *Arbutus unedo* to have survived there when *Rhododendron ponticum* could not do so, for the latter is much the hardier plant. Incidentally, it must not be overlooked that if the *Arbutus* could have persisted in or near western Ireland throughout the Ice Age, then most other members of the present British flora could have done likewise.

When all the evidence is considered it seems certain that *A. unedo* could not have survived through the Quaternary Ice Age in or near the British Isles, and consequently its presence in western Ireland at the present time must be attributed to post-glacial immigration.

Among students of post-glacial climates there is general agreement that between the end of the last phase of the Ice Age and the present day there was a long period when the climate of north-western Europe was considerably warmer than it is now. Estimates of the duration and nature (that is, to what extent it was warm and dry, and to what extent warm and moist) of this so-called 'Atlantic' period vary. Thus Gross (1931, p. 195) places it between 7800 and 3000 B.C., whereas Movius (1940) suggests 5600–2500 B.C., but all authorities agree on two points, that it was a warm period and that it occupied at least 3000 years. There is also general agreement that this warm period was succeeded by climatic conditions cooler than those of the same areas at the present time.* The conditions in the 'Atlantic' period would have facilitated the extension northward of the distribution of *A. unedo*, presuming that the species was confined to southern Europe during the glacial epoch, and the only question that arises is whether or not the warmer period was sufficiently long to allow the *Arbutus* to extend its range from, say, south-west France to southern England and Ireland? We have no data on the rate of distribution of *Arbutus*, and it is therefore impossible to answer this question. It does not, however, seem impossible that the *Arbutus* should have extended its range over about 700 miles of latitude in a period of from 3000 to 5000 years, and it might well have become distributed in post-glacial times through the Atlantic coastal belt of France to the British Isles. The deterioration in

* Considerations of the various views put forward are given by Godwin (1934), Sears (1942) and Zeuner (1946).

climatic conditions after the 'Atlantic' period, perhaps in conjunction with human activities, could well be the reason for the discontinuity of distribution which exists to-day.

It is with pleasure that I record my thanks to those who have been kind enough to assist me during the course of this work. I am particularly indebted to Dr W. B. Turrill, who suggested the work, for helpful advice at various stages and for reading the manuscript and making a number of suggestions for improving it. I am likewise indebted to Dr B. Barnes for valuable counsel during much of the work, and to Sir Edward Salisbury, Mr N. Y. Sandwith and Dr C. R. Metcalfe, for very kindly reading and criticizing the manuscript.

The area of the Killarney lakes belongs almost entirely to the Kenmare and Muckcross estates, but thanks to the kindness of those in charge, Mr Kennedy of Kenmare and Major Philips of Muckcross, I was given the freedom of the whole area and was thus able to make an extensive survey of the occurrence of the *Arbutus*. I have also to thank Mr Denis Doody of the Muckcross Gardens for assistance in various ways, while Dr R. L. Praeger very kindly gave me the benefit of his knowledge of the Killarney region before my first visit, thereby saving me much time and trouble.

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STUDIES ON *ASTERIONELLA*I. THE ORIGIN AND NATURE OF THE CELLS PRODUCING
SEASONAL MAXIMA

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I. INTRODUCTION

Asterionella formosa Hassall* regularly produces large spring and lesser autumnal maxima in the plankton of the more productive lakes in the English Lake District, notably Windermere, Esthwaite Water and Blelham Tarn (Ordnance Survey, 1947, sheets 35/30, 34/39). Similar seasonal changes in numbers are known from lakes and reservoirs in other temperate regions (e.g. Europe, Wesenberg-Lund, 1908; America, Whipple & Jackson, 1899; and New Zealand, Flint, 1938). As with many other plankton algae, the question arises: 'What happens to *Asterionella* between these periods of abundance and from whence come the cells which initiate them?' The problem has become obscure as a result of recent work (Chu, 1942, 1943, 1945; Pearsall, Gardiner & Greenshields, 1946; Storey, 1942, 1943, 1944) which, to some extent, supports that of Wesenberg-Lund (1908), Whipple (1894,

* There is considerable confusion between this species and *A. gracillima* (Hantzsch.) Heiberg. The present alga agrees with *A. formosa* Hassall as described by Hustedt (1938, pp. 251-2). Examination of cells from the bottom deposits of the lakes concerned and material collected by West & West (1909) leave little doubt that this has always been the dominant species. It is also almost certainly this species which is referred to in the works here discussed.

1896) and Whipple & Jackson (1899), but not that of West & West (1909) and Godward (1937).

There are two possible hypotheses (discussed further on pp. 414–16) concerning the origin and nature of the cells producing the seasonal maxima.

(a) That *Asterionella*, owing to the internal physiology of the cells or the deficiency of the medium in one or more nutrients, will not produce the observed maxima in the open water of lakes unless acted upon by environmental conditions operating elsewhere than in the open water or before the start of the period of increase leading to the maximum. When the growth period does occur in the open water, the growth rate of the cells is constant despite marked physical (and perhaps chemical) changes in the immediate environment. The close of the period of increase is due to internal physiological changes in the cells (physiological dormancy), or to depletion of nutrients, either previously accumulated in the cells or in the open water itself (e.g. silica).

(b) That *Asterionella* can, at certain times, obtain the necessary physical and chemical conditions for growth in the open water where it always occurs. The seasonal changes in numbers are due to changes in the physical and chemical conditions in the immediate environment of the cells in the open water.

The opposing views have been examined in relation to the periodicity of *Asterionella* in three lakes in the English Lake District between 1945 and 1949 inclusive, and by laboratory experiments. The choice of Windermere (north basin) as one of these is particularly important since much of the work cited above has been based on observations on *Asterionella* growing in it and of cells taken from it and cultivated in the laboratory. An attempt has been made to answer the following questions:

(1) Are live cells of *Asterionella* always present in the plankton (pp. 394–5), and will they grow vigorously when placed in a suitable environment even at times when they are not doing so in the lake (pp. 402–4)?

(2) Is there, at any time, an aggregation of cells in the littoral areas or on the bottom deposits such as Chu (1945) postulated at least by implication (pp. 395–401)?

(3) How important is the addition of cells from the inflows (pp. 398–402)?

(4) Are the cells of the dense populations the products of the division of cells of a special physiological type originating elsewhere, or do they arise from a change in the physiological condition of the cells in the open water (cf. question 1) (pp. 402–5)?

(5) Is the growth rate of the cells constant during the spring maximum and is it possible so to condition cells that a change in an environmental factor such as light, will not result in a change in the rate of growth (pp. 405–14)?

II. METHODS

(a) Collection

(i) Quantitative plankton samples

Collections were made weekly, or occasionally more frequently, at fixed buoys in the north end of Esthwaite Water, the east end of Blelham Tarn, and the south and north basins of Windermere. The depths at these collecting stations are 15, 12, 35 and 60 m. respectively. A uniform sample of the whole water column from the surface down to 5 m. was collected in the following way. A 5 m. length of rubber tube (garden hose) of 2.5 cm. internal diameter was weighted at one end and a cord somewhat longer than the tube was

attached close to the weight. After thorough rinsing with lake water, the tube was lowered slowly into the water until it was hanging vertically with the unweighted end level with the water surface, the free end of the cord being retained at the surface. The lowering did not take less than 1 min. The upper end was closed and the lower drawn up by the cord. The contents were poured into a sample bottle previously washed with lake water. All tubing used must first be tested to see that it does not affect the water passing through it due, for example, to the use of CaCO_3 as a filler.

Samples from definite depths were collected with a Friedinger water bottle.

Plankton from the centre of Congo, Gale Naze, and other bays in Windermere and Blelham Fish Pond (Appendix, p. 418) was collected at rather less regular intervals which were, however, rarely more than a fortnight. Owing to the shallowness of the water, collection was by inverting a bottle previously immersed below the surface.

(ii) *Qualitative plankton samples*

Plankton was also collected in a silk plankton net having 180 meshes to the linear inch. This was towed just below the surface until a large amount of plankton was obtained which was further concentrated in the laboratory by filtration on a Whatman no. 541 filter-paper. Each fortnight a vertical net haul was made through the 0–5 m. water column in Windermere, north basin. Similar samples were taken occasionally in the other bodies of water. Qualitative samples of the net-passing plankton (nannoplankton) were also obtained by filtering samples of water collected by the tube method or Friedinger bottle through a Whatman no. 1 filter-paper.

(iii) *Samples from the bottom deposits*

In areas free of rooted vegetation and large detritus particles, samples were collected with a simplified hand-operated version of the Jenkin surface mud sampler (Mortimer, 1941–2, p. 148). The surface was then removed with a pipette. Where this method was impossible owing to the presence of vegetation or large particles, a suction method similar to that described by Lund (1942, p. 246) was used. Samples of the surface layer of the mud were collected with an inverted funnel connected through a bottle to a suction pump. The funnel must be lowered gently to avoid disturbing the mud, and care must be taken that it does not sink too deep.

(b) *Counting*

(i) *Samples of plankton and cultures*

The algal numbers were obtained by sedimentation with a saturated solution of iodine in potassium iodide, and counting on an inverted microscope by the Utermöhl (1931) technique. The base of the glass-counting tubes consisted of a no. 2 cover-glass. A variety of cements were tried and the best was found to be polystyrene dissolved in xylol with dibutylphthalate as a plasticizer according to the formula: polystyrene, 15 g.; dibutylphthalate, 5 ml.; xylol, 30 ml. The end of the glass tube to be closed was dipped in the cement and left at laboratory temperature to harden for several days. A further amount of cement was then run round the outside of the tube at its junction with the cover-glass and the whole again left to harden. The tube was then filled with water and, after some hours, the cement inside could be peeled off since it had much the consistency of rubber. With most of the other cements used it was very difficult to clean the inside of the joint between

the cover-glass and tube without loosening or breaking the cover-glass. Since the whole of the inside of the base of the counting chamber is examined, internal cleanliness is essential. Results from counting by this method after sampling by the tube method or by bottle were examined statistically by Mr E. D. Le Cren and Miss C. Kipling. The populations counted were found to be distributed at random in the zones from which they were collected. The treatment of the sample after collection is equivalent to taking a sample—'a process which can be repeated indefinitely without adding to the variability of the resulting count' (Ricker, 1937, p. 78). Hence the magnitude of the statistical error depends on the number of organisms which are counted, and it is possible to calculate the confidence limits from a table such as that in Ricker (1937, table 1). In practice, as far as possible, seventy-five or more colonies were counted unless the population was too sparse to permit this. In the latter case, the necessary concentration of the sample commonly leads to inaccuracies due to the large amount of other algae and sediment present. Also the gain from counting much larger numbers than 100 is not commensurate with the effort involved. Full data concerning the statistical treatment of material obtained by the methods outlined above and counted by the Utermöhl (1931) method will be published elsewhere.

(ii) *Samples from the deposits*

The samples from the deposits naturally contained a considerable amount of water. They were first concentrated by settling, and the fine particles still in suspension were concentrated by filtration of the supernatant water through a Whatman no. 541 filter-paper and then added to the main mass of the deposit. Finally an aliquot was sucked into a wide-mouthed pipette, allowed to settle and one drop placed on a slide and covered with a $\frac{7}{8}$ in. square no. 2 cover-glass. A transect was taken across the cover-glass at a magnification of approximately $\times 300$ and, unless the cells were very numerous, the proceeding was repeated with a second drop of the deposit. One drop of the concentrated deposit contained approximately 0.5 ml., $\frac{1}{49}$ th of which was counted. Such counts are clearly much less accurate than those from the plankton samples. It was impossible to obtain equivalent samples from the diverse deposits, which consisted of varied proportions of particles of any given size and density. Nor were the samples from the same deposit necessarily the same at different times. However, even such approximate counts are preferable to the use of symbols and large differences are clearly shown by this method (Figs. 1, 2).

(iii) *Viability of cells*

In counting the number of live cells per colony in water or mud samples, the mean of counts on 100 colonies was taken. A cell was considered to be alive unless it was empty or the chromatophores were clearly more or less disintegrated. Examination showed (cf. Pearsall *et al.* 1946, p. 52*d*, para. 2; Chu, 1942, p. 322) that the size and shape of the chromatophores in the live cell vary considerably from time to time, but cells in which they appear as a row of small round, though brown, bodies or are no longer morphologically distinguishable have never proved viable. Cytological observations on such cells failed to show any clear nucleus, in contrast to those with well-developed chromatophores. It is clearly impossible to recognize the actual point at which death occurs.

(c) *Cultures*

For cultural work Chu's (1942) solution no. 10* was used, the A.R. chemicals being dissolved in filtered lake water with the addition of 10 ml./l. of an extract of Windermere mud (from 60 m. depth). In the laboratory, with artificial illumination (usually 80 W. fluorescent lamps), the cells divided three or four times every 2 days. This solution, sterilized, was inoculated from an unialgal culture. A clone isolated by Chu from Windermere, north basin, or one isolated by the author from Blelham Tarn were used from 1944 to 1948 and, in the last year, cells from Malham Tarn, Yorkshire. So far as is known there is no physiological difference between the *Asterionella* populations occurring in the lakes concerned. *Asterionella* was also cultured in filtered or unfiltered water from the lakes concerned without additional nutrients (see pp. 402-5).

Diverse glass containers were used, as well as some composed of other substances (p. 405). All glassware was originally cleaned in concentrated sulphuric acid and potassium dichromate, followed by a saturated solution of sodium phosphate. Cleaning for subsequent experiments was usually with the latter alone, though if a container was in use for long periods it was occasionally cleaned by the original method. In all cases the containers were thoroughly rinsed with tap and distilled water followed by sterile lake water or culture solution.

For experiments in the lake, trials with various containers and methods of suspension led to the adoption of the following technique. Glass-stoppered bottles of 100-150 ml. capacity were completely filled with culture solution containing an inoculum from a laboratory culture in its phase of exponential growth. The bottles were suspended at desired depths in pairs on a waxed rope attached to a buoy. The bottles were fixed together with four rubber bands and the stoppers secured with wire. The period of immersion was, usually, 1 week and never longer than a fortnight. When growth is rapid, it was found that longer periods may result in depletion of one or more nutrients, while epiphytic algae grow on the outside of the bottles necessitating frequent cleaning. To ensure that the cells used were actively growing before suspension in the lake (cf. Jenkin, 1937, p. 319) and would continue to do so under favourable conditions, a subculture in the same culture solution was made from the laboratory culture used and placed in front of a standard 80 W. fluorescent tube. The inoculum varied from week to week, but usually gave a density in the bottles of less than 200 cells per ml. Experiments showed that, under favourable light conditions, exponential growth would continue until the density in the bottles was approximately 50,000 per ml. One of the bottles was kept in the dark in the laboratory. This was necessary since divisions begun in the light or separation of cells which had already divided, might take place even in bottles suspended at levels at which there was insufficient light for the initiation of further divisions (see also p. 409).

III. THE LAKES INVESTIGATED†

The north and south basins of Windermere are separated by an area of relatively shallow water containing a group of islands (Mill, 1895). Though qualitatively similar in chemistry

* $\text{Ca}(\text{NO}_3)_2$, 0.04; K_2HPO_4 , 0.01 or 0.005; $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$, 0.025; Na_2CO_3 , 0.02; Na_2SiO_3 , 0.025; FeCl_2 , 0.0008. All g./l.

† For further data see Pearsall (1930, 1932), Pearsall and Pearsall (1925) and Mortimer (1941-2). Maps of the area in which collections were made are given in Ordnance Survey 1947, sheets 35/30, 34/39, Godward (1937), Macan (1938) and Jenkin (1942).

and biology, they differ quantitatively and in the time of occurrence of some of the main events (e.g. spring maximum of *Asterionella*; autumn overturn). They have, therefore, been treated separately. In general, the south basin which, besides north-basin water, receives the outflow of Esthwaite Water (q.v.) and sewage from the main centres of population (Windermere Town and Bowness) adjacent to the lake, is more productive than the north basin. Maps of Esthwaite Water and Blelham Tarn are given by Mortimer (1941-42, pp. 284, 180). They are both somewhat silted, but while the phytoplankton of Esthwaite Water is dominated by Myxophyceae and diatoms, that of Blelham Tarn is dominated by flagellates and diatoms except during the drier periods of summer when *Sphaerocystis schroeteri* agg. may be abundant. Windermere south basin is similar to Esthwaite Water apart from the greater number of desmid species and of colonial Chlorophyceae. Windermere north basin is the least productive of the four bodies of water, containing fewer Myxophyceae than the south basin or Esthwaite Water and fewer flagellates than Blelham Tarn. In nearly all the years for which there are records (West & West, 1909; Pearsall & Pearsall, 1925; Pearsall, 1932; Storey, 1942; and unpublished data*) *Asterionella formosa* Hass. is the dominant diatom in the plankton of the three lakes over a considerable part of the year. In the case of Windermere this appears to have been so for some 150-200 years (Pennington, 1943).

IV. THE OCCURRENCE OF *ASTERIONELLA*

(a) In the open water (Table 1)

Table 1. Number of occasions of sampling the 0-5 m. water column on which live cells of *Asterionella* were present or absent during four years

Lake	Period	Present	Absent
Windermere, north basin	31 Dec. 1944-4 Apr. 1949	250	5
Windermere, south basin	28 Feb. 1945-6 Apr. 1949	208	4
Esthwaite Water	5 Feb. 1945-5 Apr. 1949	274	1
Blelham Tarn	22 Mar. 1945-5 Apr. 1949	252	1
	Total	984	11

Up to the end of 1945, samples, apart from fortnightly net hauls through the top 5 m. in Windermere north basin, were collected by the tube method only. Whereas the tube samples average about 1 l. in volume, the net samples contained material from several hundred litres, except during large algal maxima when the meshes soon became clogged.

On three occasions, when apparently absent in Windermere north basin, Friedinger water-bottle samples from below 5 or 10 m. contained live cells. Judging from samples taken weekly at various levels down to 60 m. depth in the central area of Windermere north basin in 1947, and to 10 m. depth in Blelham Tarn in 1947 and 1948, live cells are always present in the lower layers. That this is probably true of the other two bodies of water is borne out by occasional vertical series of samples taken in them. The other eight absences (Table 1) were recorded on occasions when tube samples only were taken. Since it may be regarded as almost certain that the examination of larger volumes of water would have revealed the presence of the species on these occasions also, it is probably true to say that live cells of *Asterionella* were present on all 995 occasions of sampling. It is, therefore, unnecessary to postulate a marginal or bottom-deposit origin of the cells

* Lodged in the library of the Freshwater Biological Association.

producing the growth periods unless one of the hypotheses set out on p. 390 can be shown to be true.

The production of cells in a certain locality might be expected to lead to an aggregation there, at least for a time. Further, the population density in such a locality might be expected to be relatively high before the increase in the open water if these populations produce the cells which later form the great maxima in the open water. Attempts were made to find such localities and aggregations of cells. The bottom deposits were sampled in the regions enumerated in the Appendix (p. 417) for a year or more, usually at weekly or fortnightly intervals.

(b) *On the deposits* (Figs. 1, 2)

Figs. 1 and 2 show the numbers of live *Asterionella* cells in the plankton and on the deposits of Windermere and Blelham Tarn. The station in Sawpit Bay (Appendix A, 1 (c); Godward, 1937, Fig. 1a, F-H) lies off a relatively exposed shore and that in Pull Wyke Bay (Appendix A, 4 (d), Godward, 1937, P.W.1) close to a very sheltered shore. It was not possible to count dead cells since all the deposits are more or less rich in frustules from previous growth periods of *Asterionella* (cf. Pennington, 1943). In all cases the changes in numbers on the deposits follow closely those in the plankton. The fact, too, that they are fewer on the shallower, more sheltered deposits suggests that the cells originate in the plankton. All the other littoral deposits examined gave similar results; so did occasional observations on the mid-lake deposits. In the spring the maximum on the bottom, particularly in the profundal areas, usually follows that in the plankton after an interval owing to the fact that the water is stratified at this time. The cells then tend to be held by water movements in the epilimnion and must sink through the thermocline and hypolimnion before reaching the bottom. In the late autumn and winter, when the lake is isothermal, cells are carried rapidly to the bottom by water movements and the time lag is less (Fig. 2). The long period early in 1947 with no living cells on the bottom in Blelham Tarn (Fig. 2), despite a considerable population in the upper layers of the water, was due to the inverse thermal stratification which developed during several weeks of ice cover. This led to the disappearance of dissolved oxygen from the bottom water which thus became lethal to *Asterionella*. Water containing live *Asterionella* cells was placed in bottles containing surface mud from 15 m. depth in Blelham Tarn and the bottles closed. In every case all the cells died within a few days. A few experiments with Windermere north basin and Esthwaite Water muds from the deep areas gave the same results. It is clear, therefore, that the cells cannot live under the reducing conditions such as occur in these bottles and in the deeper regions of Blelham Tarn and Esthwaite Water every summer, and when prolonged ice cover is present in winter (Mortimer, 1941-2). When a plentiful supply of free oxygen is present, however, the mud is not lethal, and growth can be obtained from cells on the surface in illuminated biphasic cultures with these muds (Pringsheim, 1946). In the littoral areas (0-10 m.), however, water movements and the activities of other organisms (including man) lead to a more or less frequent disturbance of the mud surface. On burial, *Asterionella* has no means of its own of regaining the surface. Experiments showed that if such disturbance and burial were simulated in the laboratory, the cells soon died. It is of interest that the rich and varied population of algae inhabiting the surface mud in the littoral, which alone receives sufficient light to permit growth (cf. Pearsall *et al.* 1946, Fig. 2), consists almost exclusively of algae able to return to the surface after burial. Since, at or after periods of high numbers in the plankton,

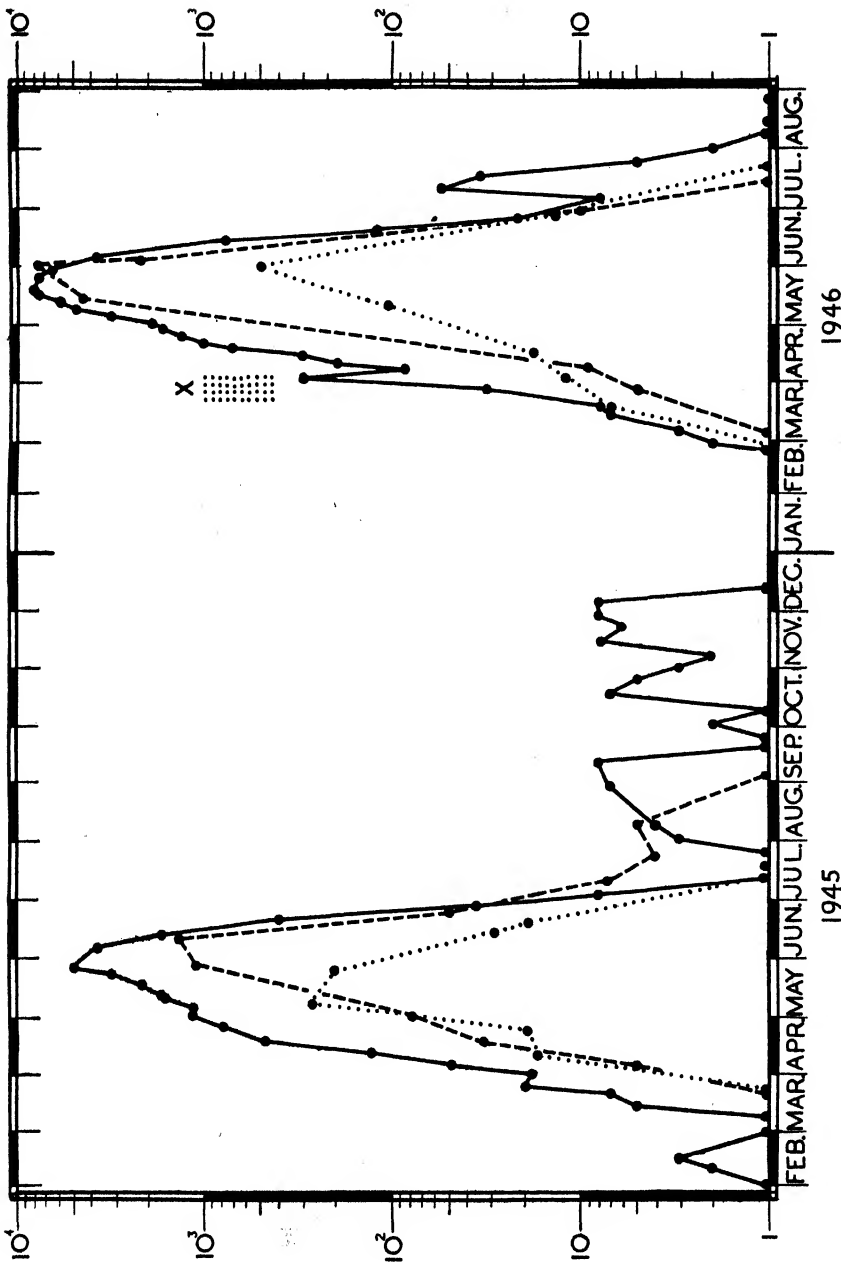


Fig. 1. Live cells per ml. of *Asterionella* in Windermere north basin, plotted on a logarithmic scale (vertical axis); in the 0-5 m. water column at the central buoy (Appendix A, 8)—continuous line; on the surface of the lake bottom in Sawpit Bay at 3.5 m. depth (Appendix A, 1 (c))—interrupted line; on the surface of the lake bottom in Pull Wyke Bay at 0.25 m. depth (Appendix A, 4 (d))—dotted line. Time scale, horizontal axis. For methods of estimating the number of cells on the bottom for Figs. 1 and 2 see p. 392. At X stippled column marks the period of temporary stratification referred to on p. 414.

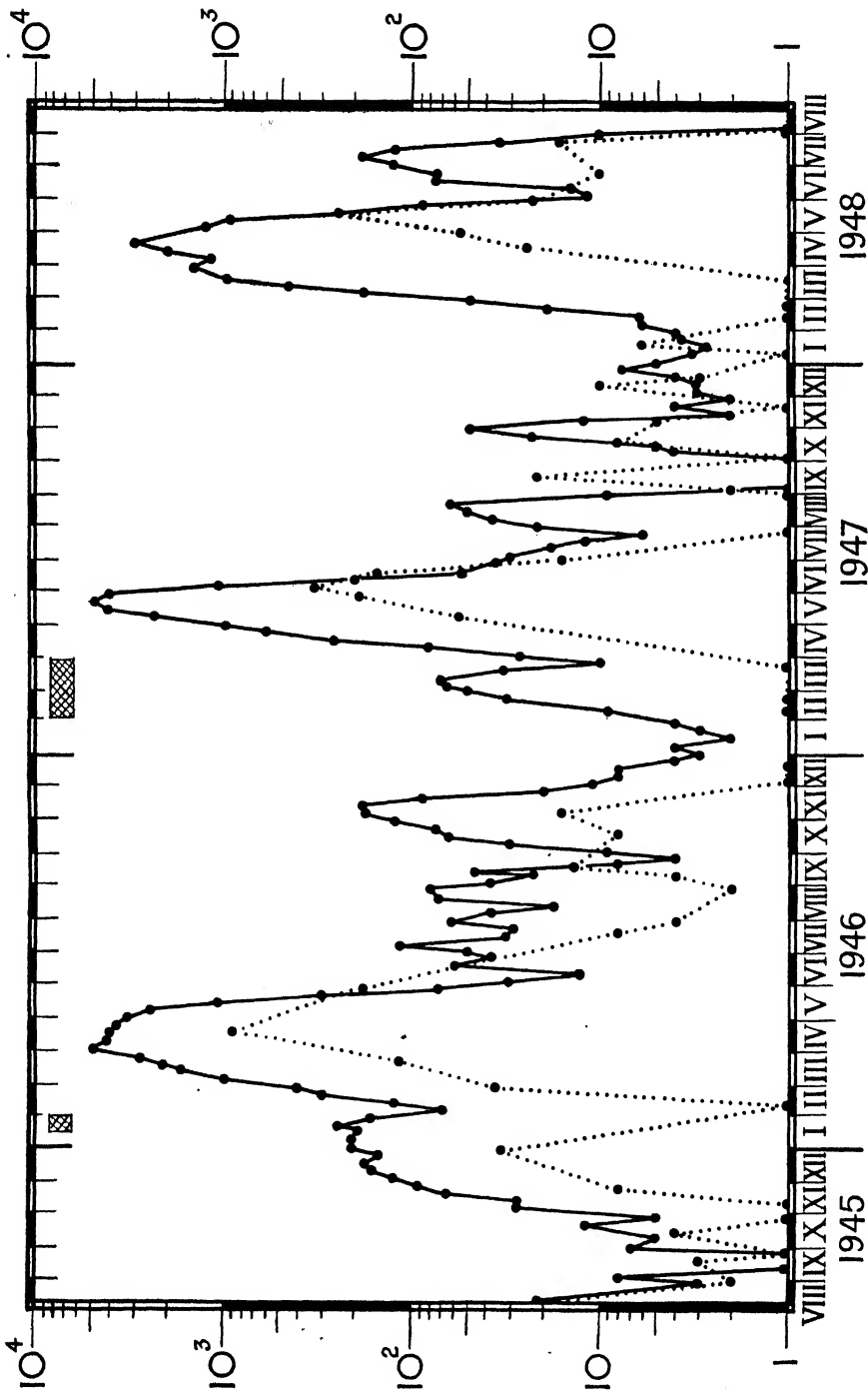


Fig. 2. Live cells per ml. of *Asterionella* in Belham Tarn, plotted on a logarithmic scale (vertical axis), in the 0-5 m. water column at the buoy (Appendix B, 1)—continuous line; on the surface of the lake bottom at 15 m. depth (Appendix B, 2)—broken line. Time scale, horizontal axis; the lake was covered by ice during the periods covered by the cross-hatched areas at the top of the graph.

high densities of *Asterionella* cells occur on the deposits, it can hardly be argued that cells, continuously produced in such areas, would always be carried out into the open water so rapidly that aggregations would never be formed on the deposits.

The evidence points, therefore, to the littoral and profundal* deposits receiving cells from the plankton, but does not suggest that they act as centres of production of cells later carried out into the plankton (see also Godward, 1937, pp. 529-30).

(c) *In the plankton of sheltered areas* (Figs. 3, 4)

Fig. 3 shows the number of live cells of *Asterionella* in Gale Naze Bay (Appendix A, 7; Godward, 1937, fig. 1a, Str. 7.2), and at the central buoy of Windermere north basin (Appendix A, 8). The numbers at both places are very similar, the major differences being due to seiches and inflow. Gale Naze Bay lies at the north end of the lake near the main inflow (Ordnance Survey, 1947, sheet 35/40; Godward, 1937); consequently, the water in it is particularly affected by seiches (see p. 412) on the north-south axis of the lake, as occurred in June 1947 (Fig. 3), and by warm water flowing in from the river during periods of thermal stratification, and by severe floods at any time. The low numbers in Gale Naze Bay in February and March 1947 were due to ice cover followed by floods (compare Fig. 2). On the other hand, in 1948, there were appreciable numbers in the bay before the spring increase began in the open water (Table 2, Fig. 3, February); cells which might act

Table 2. *Asterionella* populations in two areas and the main inflow of Windermere (Ordnance Survey 1947, sheet 35/30) showing the similarity between those in Gale Naze Bay (Godward, 1937, fig. 1a, station 7.2) and the inflow (Godward, 1937, fig. 1a, station Br. 1) and dissimilarity between these and that at the central buoy of the north basin

Area	Live cells per 100 ml.	Dead cells per 100 ml.	Live cells per colony
Birdhouse (Rothay-Brathay) River	573	413	2.8
Gale Naze Bay	648	424	4.3
North Basin central buoy	81	10	5.6

as precursors of this growth. These cells, however, came from the inflow, and the colonies contained so many dead and apparently unhealthy cells that the population might more correctly be considered as moribund. Many cells had a peculiar appearance, somewhat similar to that produced by plasmolysis, which made it possible to recognize them as having come from the river. No cells having this appearance have ever been observed in samples from mid-lake.

Occasional samples of plankton from the centre of Pull Wyke Bay (Appendix A, 4 (a); Godward, 1937, fig. 1a) showed close agreement in population density with the samples from the central buoy. In 1945, observations on Congo Bay, Windermere (Appendix A, 6; Godward, 1937, fig. 1a, c) showed that there was a considerable population of *Asterionella* in the plankton before the numbers in the open water of the north basin had risen appreciably (e.g. eighteen times the density on 23 March). That the numbers in the bay appeared to bear a closer relation to those in Blelham Tarn (Appendix B), the outflow of which (Blelham Beck, Godward, 1937, fig. 1a) passes into it was confirmed by detailed observations in 1946 (Fig. 4) and occasional ones in 1947. For example, the density of

* The term 'littoral' here covers the zone in which light penetration is sufficient for appreciable algal growth and 'profundal' all deeper areas.

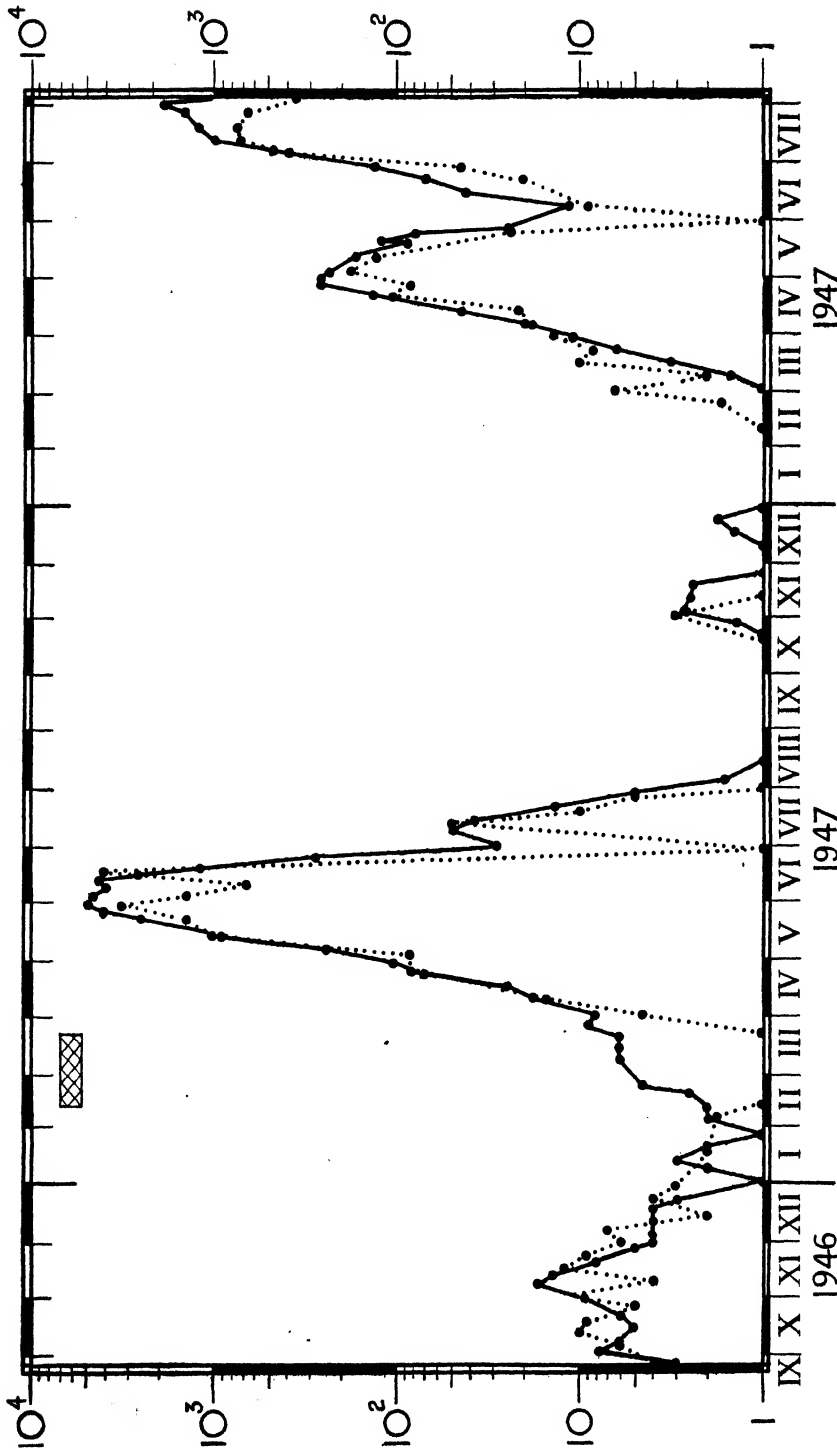


Fig. 3. Live cells per ml. of *Asterionella* in Windermere north basin, plotted on a logarithmic scale (vertical axis); in the 0-5 m. water column at the central buoy (Appendix A 8)—continuous line; in the open water of Gale Naze Bay (Appendix A, 7)—interrupted line. Time scale, horizontal axis. The cross-hatched area shows the period during which Gale Naze Bay was covered by ice.

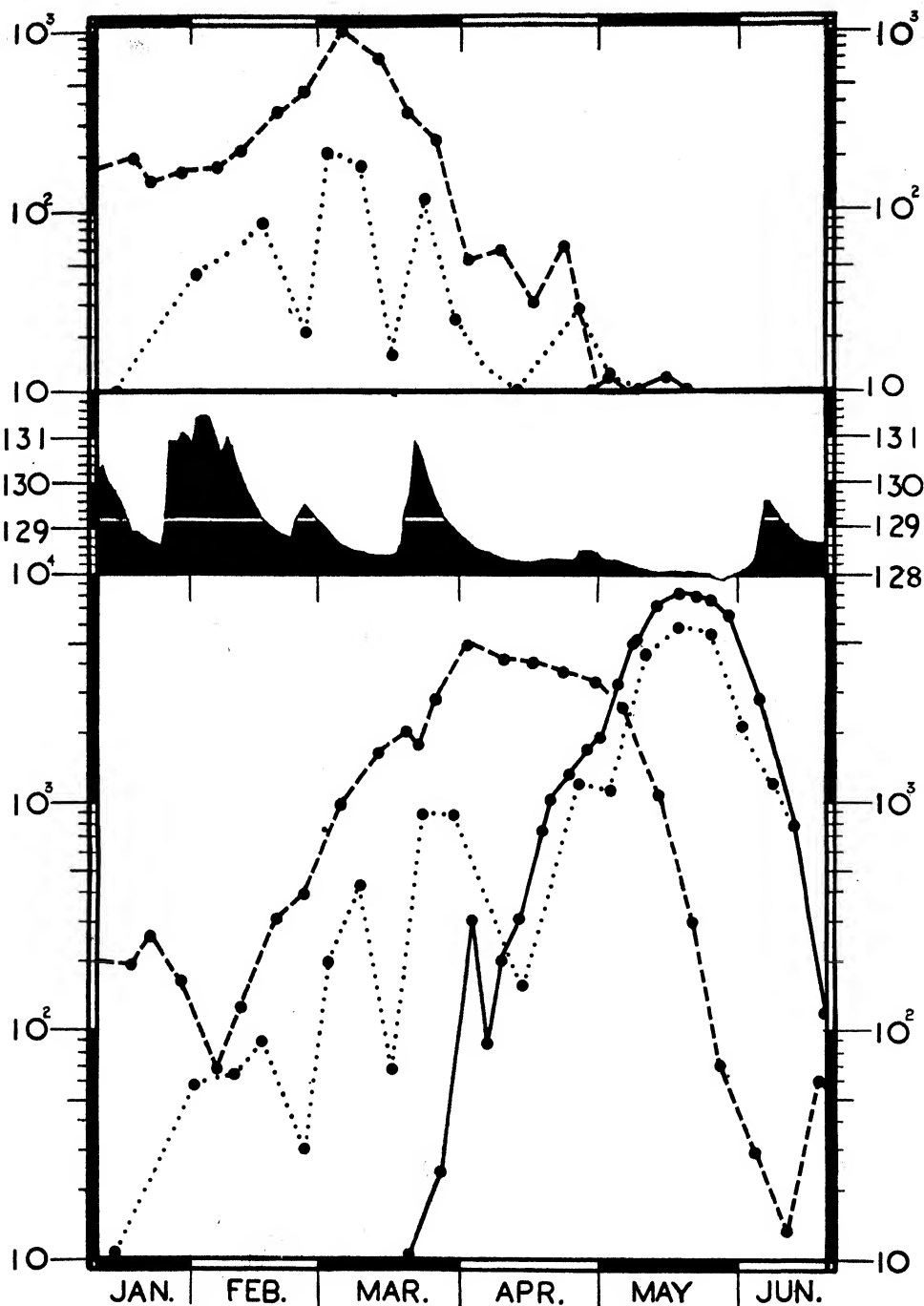


Fig. 4. Live cells per ml. of *Asterionella* and *Melosira* in Blelham Tarn and Windermere north basin in 1946, plotted on a logarithmic scale (vertical axis). Windermere north basin lake level, solid black, with mean lake level (1932-48, in feet) shown as a white horizontal line. Below lake level graph, *Asterionella* cells; in the 0-5 m. water column at the Windermere north basin central buoy (Appendix A, 8)—continuous line; in the Congo Bay (Appendix A, 6)—broken line; in the 0-5 m. water column at the Blelham Tarn buoy (Appendix B, 1)—dotted line. Above the lake level graph, *Melosira* cells plotted as for *Asterionella*. Only densities of 10 cells and over per ml. are shown. Time scale, horizontal.

Asterionella in the plankton of Congo Bay was 140 times that at the Windermere north basin central buoy on 3 March 1946, but less than in Blelham Tarn. The case of *Melosira italica* is the same; indeed this diatom only twice reached a density of over 10 cells per ml. at the Windermere north basin buoy. As the numbers of *Asterionella* decline in Blelham Tarn and rise in Windermere, those in Congo Bay follow the changes in the latter closely, though at a slightly lower population density. The changes in the average numbers of live cells per colony (see Gardiner, 1940-1) also follow a similar course in Congo Bay, being nearer the Blelham Tarn average from January to early April and nearer that of the population in the open water of Windermere north basin from mid-April to July. The changes in the lake level,* and so of flow down Blelham Beck, also bear a relation to the changes in the numbers of *Asterionella* and *Melosira* in Congo Bay. After and during flood periods the numbers rise in Congo Bay while, in the case of *Asterionella*, they may fall more or less markedly in Blelham Tarn (Fig. 4). During dry periods (e.g. 31 March-4 June 1946) the numbers in Congo Bay tend to fall even when rising or high in Blelham Tarn. That the numbers in Congo Bay should always be less than in Blelham Tarn is to be expected since there will be a loss downstream as has been shown by Chandler (1937).

In the autumns of 1945, 1946 and 1947 *Asterionella* reappeared in quantity in Congo Bay at the same time as in Blelham Tarn, although the autumn maximum in Windermere north basin never exceeded 16 cells per ml. Further, scattered analyses of Congo Bay water made between 1945 and 1948 showed that changes in the rate of inflow from Blelham Tarn, the water of which has a higher alkalinity than Windermere, could be detected by variations in alkalinity. The abundance of *Asterionella* in the sheltered Congo Bay in the late winter and early spring may provide cells for the spring growth-period that follows in Windermere north basin. There is, unfortunately, no method by which the fate of those cells and their descendants can be traced. The aggregation of *Melosira italica* in Congo Bay is not followed by an appreciable maximum in Windermere north basin.

The relationship of the Esthwaite Water plankton to that of Windermere south basin has also been studied. The outflow of Esthwaite, Cunsey Beck (Appendix H), passes into the north end of Windermere south basin. The development of *Asterionella* in Esthwaite Water takes place at about the same time as that in Blelham Tarn. Thus cells are passing from there into Windermere south basin at the same time as those from Blelham Tarn pass into Windermere north basin. If these too acted as precursors of the spring increase in Windermere south basin, it might be expected that it would start at the same time in the two basins. Actually, the south basin spring-growth period starts, on the average, a month earlier than that in the north basin. This suggests, as an alternative explanation, that the start of the spring-growth period is not due to the enrichment of the water from the drainage basin, but to factors acting on the cells in the open water of Windermere irrespective of such enrichment. This view is strengthened by data from Blelham Tarn considered in the next section.

(d) *In the drainage system—Blelham Tarn*

Asterionella cells have been shown to pass into both basins of Windermere from the drainage system (via Grasmere, Rydal Water, Elterwater, Blelham Tarn and Esthwaite Water—Ordnance Survey, 1947, sheets 35/30, 34/39). Esthwaite Water also receives the outflow of several tarns, notably Wise E'en on Claife Heights (Ordnance Survey, 1947,

* The level of Blelham Tarn fluctuates similarly, but more rapidly than that of Windermere north basin.

sheet 34/39) and Priest's Pot (Appendix F). Occasional observations show that small numbers of *Asterionella* may be present here, but densities exceeding 20 cells per ml. have never been observed. In the catchment area of Blelham Tarn there is only one body of open water where *Asterionella* might be expected to grow, namely Blelham Fish Pond (Appendix C). *Asterionella* is very rarely seen in small bodies of water such as pools, puddles or ponds, nor does there appear to be any record of it occurring in abundance in such habitats. Nevertheless, the drainage basin of Blelham Tarn has been extensively searched between 1945 and 1948, but no specimens have been found. In the case of Blelham Fish Pond some fifty plankton samples collected at irregular intervals from March 1945 to March 1948, and including every month of the year, contained no *Asterionella* colonies. The only sources of inoculation from outside, therefore, are aquatic birds and insects, and it seems unlikely that these could carry enough live cells to affect the seasonal cycle appreciably. Despite this absence of *Asterionella* from outside sources the seasonal cycle in Blelham is of the same basic type as in Windermere and Esthwaite. Further (p. 395), no signs of any aggregation in the reeds or on the deposits have been observed. This suggests strongly that the periodic increases of *Asterionella* in Blelham Tarn depend on the cells which are always present to a greater or lesser extent in the open water of the lake. If this be so in Blelham Tarn, there seems no reason why it should not also be the case in the other lakes.

V. RESTING STAGES

Like all other workers I have never observed any morphologically distinguishable resting stage. In view of the abundance of *Asterionella* in many parts of the world and the large number of collections containing it which have been examined, it seems almost certain that no such stage exists. The same is true of the almost equally common and widespread plankton diatoms *Tabellaria fenestrata* (Lyngb.) Kütz., *Fragilaria crotonensis* Kitton and some *Melosira* spp. (Wesenberg-Lund, 1908, pp. 51-54). There remains the possibility that the physiological state of the cells may vary at different times of year (Storey, 1943, 1944). This is almost certainly the case but, so far as my observations go, there is no evidence of the population as a whole passing into a state of dormancy. Miss B. M. Knudson, while working as my assistant, has shown that *Asterionella* cells can remain alive in the dark for at least 5 months if the water contains free oxygen. Under such conditions, and in cultures kept in the dark for a few days to a week or so, she and I have observed that the chromatophores decrease in size. On being replaced in the light such cells take a day or two to pass from this state, in which no multiplication occurs, to the state in which the chromatophores enlarge and growth at the maximum rate attainable in the conditions of the experiment is resumed. As, however, chromatophore size is also affected by other environmental conditions, it is not possible to distinguish cells which have been affected by prolonged darkness in nature. Whether or not some cells pass into a state of dormancy of the type described by Storey (cf. pp. 403-5) would need a more detailed examination. So long as a reasonable proportion can grow under favourable conditions, dormancy alone cannot be the cause of the catastrophic drop in numbers which marks the end of the spring period of increasing numbers, nor can it explain the failure of the population to increase before or after the autumn maximum. Table 3 shows the number of times *Asterionella* populations in samples taken from the central areas of the lakes investigated (mainly Windermere north basin) grew, with or without enrichment, in

diverse containers (glass, celluloid, perspex and polystyrene) in the laboratory, or suspended in the lake in different months of the year. Other algae were also present. The containers were usually opened a week after inoculation. Various methods were used because the experiments were designed for other purposes besides testing the ability of the cells to multiply.

Table 3. *Number of occasions each month when Asterionella cells in lake water taken from the central areas of Windermere, Esthwaite Water and Blelham Tarn grew or failed to grow in unenriched lake water (L.W.) or lake water enriched with salt solutions (C.F.). For details of tests see above*

Month	Growth		No growth	
	L.W.	C.F.	L.W.	C.F.
Jan.	5	1	1	0
Feb.	7	1	0	0
Mar.	6	1	1	0
Apr.	11	0	0	0
May	14	6	4	1
June	9	23	1	0
July	3	3	0	0
Aug.	2	4	0	0
Sept.	3	3	0	0
Oct.	2	1	0	0
Nov.	5	2	0	0
Dec.	8	0	1	0
Total	75	45	8	1

In every month growth can occur. In six of the cases where there was none, only lake water was used. *Asterionella* multiplied in all but one of the samples enriched with culture solution.

It is clearly desirable that Storey's experiments (1943, 1944, and cf. p. 402) be repeated. One of the difficulties of obtaining data on one or a few colonies, as in her experiments, at the end of the spring maximum and during the decline in numbers, is that most of the cells are dead or dying. It is also curious that no such physiological state, as postulated by Storey, has ever been detected in the laboratory cultures. These are often grown to a standstill but it is possible to subculture them, when active growth is resumed. If populations are subcultured during the exponential phase of growth they continue to grow exponentially, though a lag period of relatively slow growth rate may occur during the first 24 hr. after subculture. This has been done over periods of several months, and it appears that the cells can be kept growing exponentially for an indefinite period. Moreover, on a number of occasions, growth in the bodies of water investigated has begun again after the spring maximum, interrupting the usual sharp decline in numbers. In Blelham Tarn some growth occurs at various times between the end of the spring maximum and the start of the autumn growth period. In Blelham Tarn and Esthwaite Water growth occurs throughout the autumn and winter. Samples from the populations in these lakes have been examined and also grown in the laboratory under varied conditions, and there is no evidence that the individuals composing them belong to a different strain from those in Windermere.

The experiments described above show that, contrary to the experience of Chu (1945), *Asterionella* can grow in unenriched water taken from the central areas of all these lakes over a considerable period of the year. While it might possibly be objected that the water was slightly enriched by solution of substances from the walls of the glass containers,

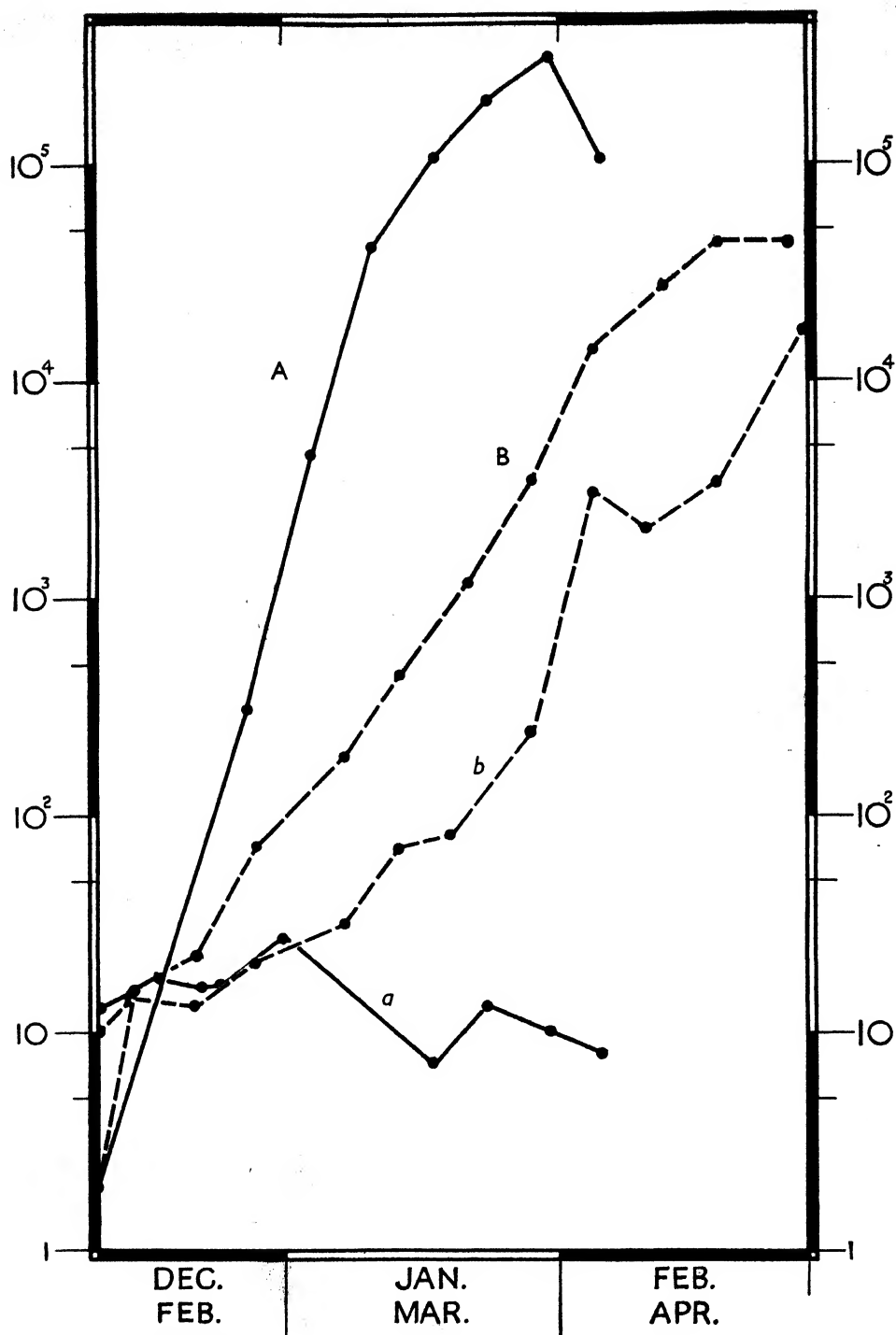


Fig. 5. Growth of *Asterionella* in Windermere north basin water in the laboratory (p. 405), and the lake itself. Left-hand upper lines, growth in two experiments: A (continuous line), B (broken line) in glass tanks containing 12 l. of lake water, 10 of which are renewed weekly, illuminated by one 150 W. lamp. Right-hand lower lines, density of the population in the 0-5 m. water column at the Windermere north basin buoy (Appendix A, 8) during the period covered by Exps. A (continuous line *a*) and B (broken line *b*). All cells per 10 ml. plotted on a logarithmic scale (vertical axis). Time scales, horizontal axis, for first experiment (A, *a*) above; second (B, *b*) below.

similar vessels were used by Chu, and growth also occurs in celluloid, perspex or polystyrene containers. Moreover, if fresh supplies of lake water are added at intervals, large growths can be obtained in the laboratory. Fig. 5 shows the growth made in glass tanks in the laboratory, illuminated by 150 W. lamps. The inoculum consisted of 2 l. of Windermere north basin surface water to which were added 10 l. of filtered surface water. Each week 10 l. of the water in the tank were removed. The *Asterionella* cells were filtered off and washed back into the tank with filtered lake water. Sufficient lake water was then added to restore the volume in the tank to 12 l. A certain number of cells were naturally lost in the process, but maxima as big as, or bigger than, those recorded for Windermere north basin were produced in these tanks and this despite the growth of other diatoms present in the inoculum, mainly *Synedra* spp., which reached 22,000 cells per ml. in one experiment and 14,000 in the other. During the first experiment no increase of *Asterionella* took place in the lake, there being 13 cells per 10 ml. on 10 December 1945 and 8 per 10 ml. on 5 February 1946. The period of the second experiment was, in part, synchronous with the spring period of increase in the lake, but the steady rise in numbers in the tank bore no relation to the irregular rise in the lake. The ability to grow would appear to be governed not only by the concentration of salts at any one time but also by the rate of supply which, in the lake, will be a function of turbulence (cf. Lund, 1947).

In each of the experiments described and illustrated in Fig. 5, a control tank was set up in the same way but the water in it was never renewed. Growth in these untouched tanks was only about 1% of that in the others. Thus, a large growth can be produced in the laboratory (Exp. A, Fig. 5) in Windermere water taken in winter, some months before the period of increase in the lake starts, solely by illuminating it. This suggests that, contrary to the suggestion of Pearsall *et al.* (1946, pp. 19–20), growth in the open water is intimately related to factors operating in the immediate environment at any one time. Further data on this point are discussed in the following section.

VI. GROWTH RATE

(a) Increase in numbers in the lake at different levels (Fig. 6)

Pearsall *et al.* (1946) and Storey (1942) pointed out that the rate of increase of *Asterionella* in Windermere north basin and elsewhere appeared to be constant over a considerable part of the spring period of increase despite rising light duration and intensity and temperature. This suggested that the rate of growth of *Asterionella* was unaffected by these variations in the immediate environment. I believe that their data can be more satisfactorily interpreted somewhat differently.

If growth were constant, despite variations in light and temperature, we should expect equal growth at all depths in material taken from a population previously growing under the same conditions. Yet marked changes occur in Windermere north basin once stratification sets in (Fig. 6, right-hand side of stippled vertical column). In the early part of the growth period the lake is isothermal and the population increase rate* is the same at all depths (Fig. 6, left-hand side of stippled vertical column). With the onset of thermal stratification (Fig. 6, period covered by vertical stippled column) the upper warmer photic zone (epilimnion) and lower colder dark zone (hypolimnion) are separated from one another by the zone of temperature discontinuity (thermocline, see Welch (1935) for this and other

* This is not equivalent to the growth rate of the population, see p. 412.

limnological terms). If the growth rate were constant, despite changes in temperature and illumination, we should expect the cell numbers to increase in the epilimnion and hypolimnion at least during the early part of stratification. In fact (Fig. 6) the increase below the thermocline is immediately arrested. Yet, *Asterionella* cells, in samples from the

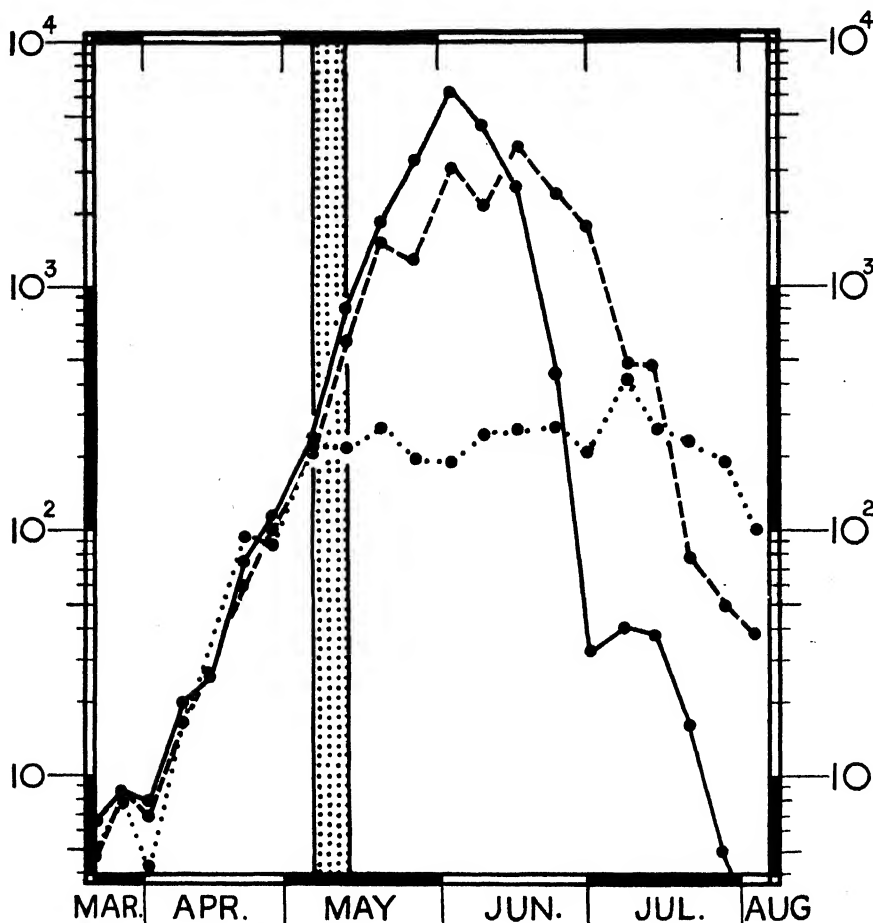


Fig. 6. Live cells per ml. of *Asterionella* plotted on a logarithmic scale (vertical axis) in Windermere north basin water samples (in 1947) taken at the central buoy (Appendix A, 8); at 2 m. depth—continuous line; at 10 m. depth—broken line; and at 40 m. depth—dotted line. Vertical cross-hatched column, period between isothermal and stratified conditions. Time scale, horizontal axis.

Table 4. The ranges of certain nutrients in mg. per litre for active growth of *Asterionella* in cultures made by Chu (1942, p. 322) and those of Windermere north basin water between 1945 and 1949 inclusive

	Culture	Windermere
SiO ₂	9.8–19.6	0.2–2.5
P. PO ₄	0.18–9.0	<0.001–0.004
N. NO ₃	1.7–17.0	0.04–0.40

hypolimnion taken at various times after thermal stratification had set in, grew actively in the laboratory when illuminated. Since no nutrients were added, this suggests that lack of light is what inhibits growth in the hypolimnion. Whipple (1896, pp. 157–8, fig. 5)

obtained similar results in a lake about 18 m. deep, though there was sufficient light for some growth in the thermocline and below during the early stages of stratification (compare his fig. 5 with figs. 1 and 3). The observations on populations from the lakes studied are not,

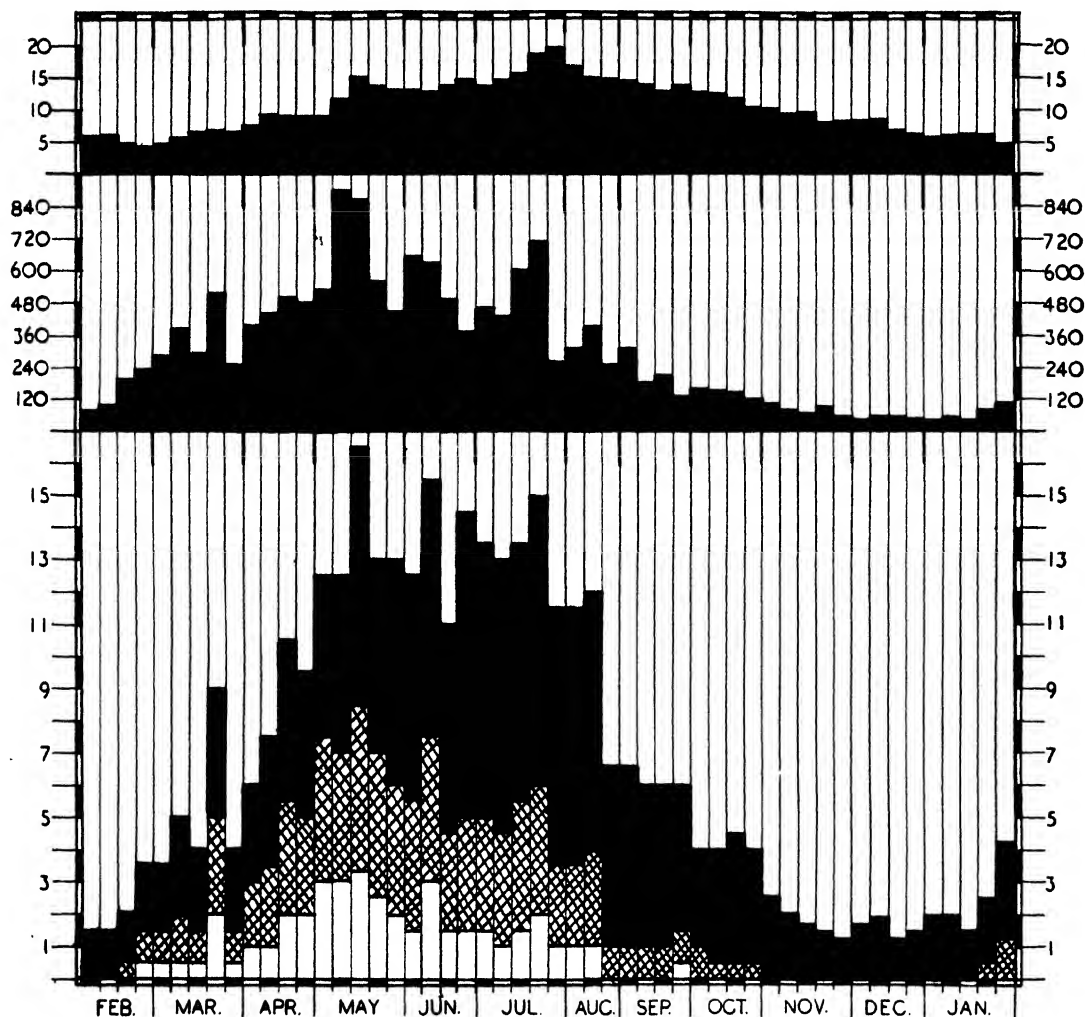


Fig. 7. Growth of unialgal cultures of *Asterionella* in glass bottles suspended for 1 week from the Windermere north basin buoy (Appendix A, 8). Lower histograms, growth expressed as number of synchronous cell divisions (to nearest half-division) per week at 0.5 m. depth (solid black), 5 m. (cross-hatched) and 7 m. (unshaded). Central histograms, mean amount of light per day in kilolux hours and upper histograms, mean daily surface temperature at °C. during each weekly experiment. Horizontal axis, dates of start of each experiment. The measurement of light was made possible by an apparatus devised by Dr C. H. Mortimer connected to a photo-cell on the main tower of Wray Castle. In view of the difficulties in obtaining an accurate figure (see Poole & Atkins, 1936) the absolute values must be considered as approximate pending final calibration.

however, conclusive. In them the epilimnion is also the zone in which there is sufficient light for photosynthesis. Owing to turbulent mixing the population in the epilimnion is more or less evenly distributed, and so it is impossible to demonstrate any progressive

decrease in increase rate with increasing depth. It may well be argued, therefore, that this observation does not disprove the constancy in growth rate under varied light conditions since it only shows the effect of plunging a growing population into virtual darkness.

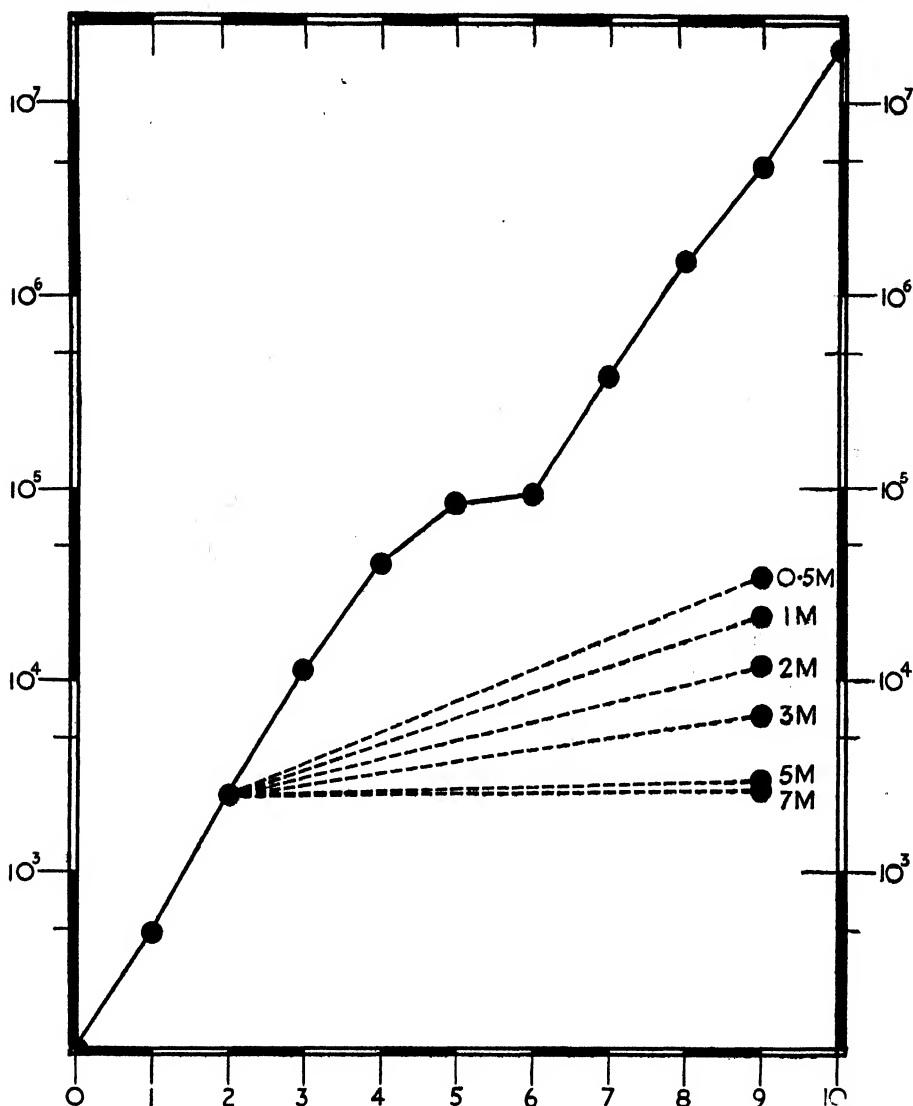


Fig. 8. Growth of unialgal cultures of *Asterionella* in glass bottles, made from the same inoculum, in the laboratory—continuous line—and suspended from the buoy in Windermere north basin (Table 3, Appendix A, 8) at various depths—broken lines. The growth rate of the culture in the laboratory is reduced between days 5 and 7 owing to utilization of the available nutrients, and on day 7 a subculture was made into fresh but identical culture solution. All cells per ml. plotted on a logarithmic scale (vertical axis). Time in days, horizontal axis.

Further, the changes at 10 m. are connected with the turbulence changes due to this level lying for a greater or lesser part of the period in the thermocline zone. Experiments with unialgal cultures in glass bottles suspended at various depths have also been carried out (Figs. 7, 8). A laboratory culture of *Asterionella* was continuously illuminated in glass

bottles on a glass sheet above a fluorescent light. Each week subcultures were made and suspended from the Windermere north basin buoy at various depths as described on p. 393. Fig. 7 shows the amount of growth expressed as the number of synchronous divisions made by the population in the bottles during the period of immersion. It is, therefore, a measure of growth rate. It shows that cells kept under closely similar laboratory conditions for the duration of the experiment grow at different rates as soon as the environment is changed. The growth rate is least when the illumination and temperature are lowest, and highest when these are highest. Moreover, in any one set of bottles, growth varies in relation to their depth of suspension. The results of Whipple's (1896) experiments using natural populations are very similar. Fig. 8 shows, in addition, the growth rate in a bottle in the laboratory in which the cells were counted daily throughout the period of experiment. All the bottles were filled with the same stock culture solution. This emphasizes the very marked change in growth rate with immersion of the culture in the lake. Bottles were suspended at the same depths and for the same periods in Esthwaite Water and Blelham Tarn. Apart from the bottle at 0.5 m. during a part of the summer, growth is greater at a given depth in Windermere north basin than in Esthwaite Water or Blelham Tarn. This is to be expected if an immediate change in growth rate takes place with a change in environmental conditions as light penetration is greater in Windermere than in the other two lakes. In Esthwaite Water and Blelham Tarn it is almost the same though, in autumn, it may be less in Esthwaite Water owing to the large growths of *Myxophyceae* which only occur sparsely in Blelham Tarn.

(b) *Growth in the laboratory under varied conditions* (Figs. 9-11)

Cultures were made in the laboratory and grown under different or changing conditions of light, temperature and nutrient concentration. The methods of culture are described on p. 393. Fig. 9 illustrates changes in relation to light intensity. In each experiment, increasing light intensities lead to an immediate increase in growth rate, though the growth during the first day after the change was less than on succeeding days. This lag period was most marked where the change was from conditions where the illumination was so poor as to lead to no appreciable growth (upper graph, Fig. 9) to those where the full rate was more than two divisions per day. In both experiments there was also an increase in growth rate in the fully illuminated bottles in the latter half of the experiment. This can be related to the decrease in volume of fluid in the bottles resulting from the daily removal of samples. In the latter half of the experiment the cells were all nearer the light, and the reduced volume of water may also have led to an increased rate of diffusion of CO_2 into the culture fluid.

Decreased illumination also led to decreased growth rate. In the experiment illustrated in the upper graph (Fig. 9) some growth took place during the first day of reduced illumination. By counting the proportion of the cells in the process of division (that is cells in which new walls could be seen) before shading the bottles, it appeared that this can be explained by the completion of these divisions and separation of the daughter cells so formed. The change in growth rate was therefore even sharper than is suggested by the graph, since few if any further cells started divisions after the cultures were darkened. The initial increase in illuminated cultures of *Nitzschia closterium* on transference to darkness, described by Riley (1943), may be explicable in the same way. His cultures showed the greatest subsequent growth in the dark when the photosynthetic rate had been highest.

This may well also be the time when the greatest proportion of the population were in the process of division before transference to the dark.

Fig. 10 shows the effect of varying the temperature of the culture solution. The experiment was carried out in a similar manner to the previous, except that one or other set of bottles was cooled by a stream of water. Illumination was identical in a control experiment and bottles in static water showed the same growth rate as those not

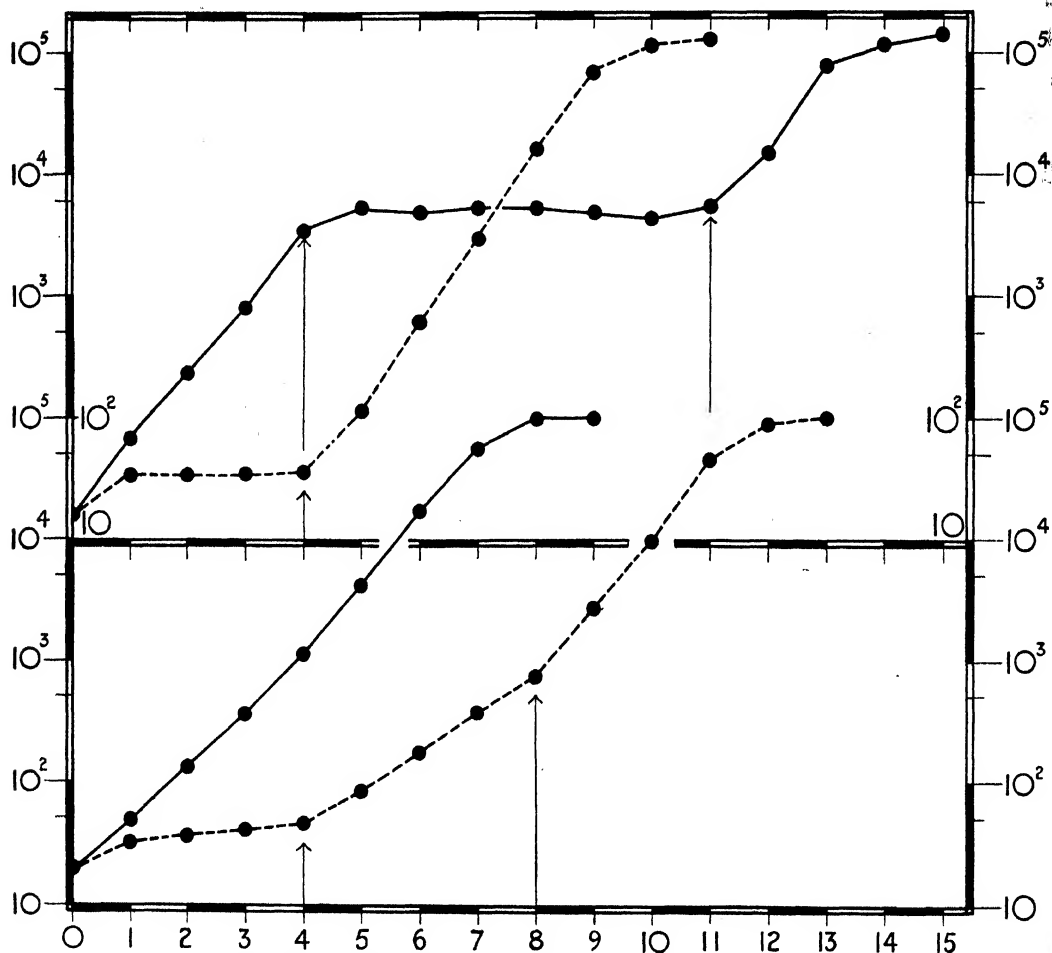


Fig. 9. Growth of *Asterionella* in unialgal cultures in the laboratory with varied light intensities. Upper graph: continuous line, bottles unshaded days 0-4 and 11-16, shaded by ten Whatman no. 5 filter-papers placed between them and light from days 4 to 11; broken line, bottles shaded by ten similar filter papers, days 0-4, bottles unshaded, days 4-11. Lower graph: continuous line, bottles unshaded; broken line, bottles shaded by five filter-papers, days 0-4, by two filter-papers, days 4-8 and unshaded, days 8-13. All cells per ml. plotted on a logarithmic scale (vertical axis). Time in days, horizontal axis.

in water. The difference between the two sets of bottles used was about 10-11° C. On the fourth day the two sets of bottles, and so the temperature of the water within them, were interchanged; as with light, an immediate change in growth rate took place.

As is to be expected, varying the concentration of the nutrient solution made no change in the growth rate during the exponential phase (Fig. 11). Chu (1942, p. 320), however,

claims that it does. So long as the cell has a superabundance of nutrients the rate of growth will depend on physical factors such as light and temperature. Only when the supply of nutrients becomes too slow to enable the cell to grow at the rate dictated by the physical conditions will the chemical conditions control the growth rate. This effect is,

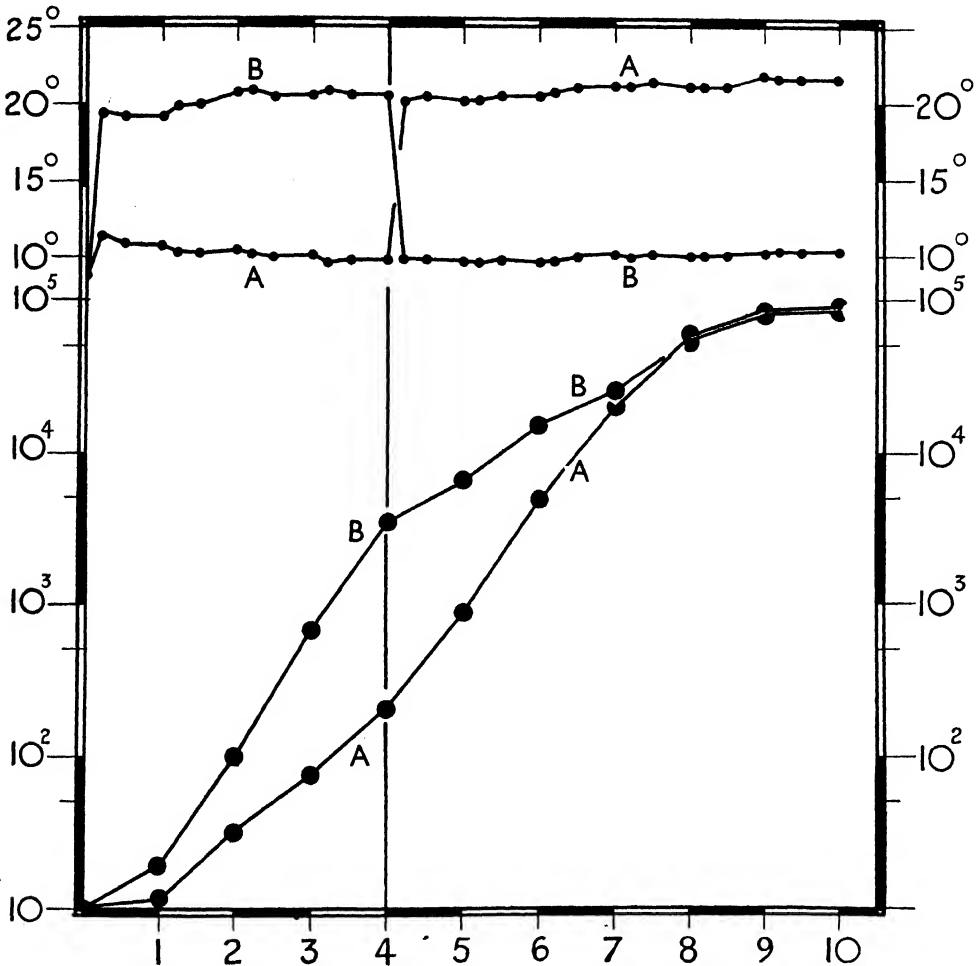


Fig. 10. Growth rate of *Asterionella* in relation to temperature. One set of bottles (line A) cooled from days 0 to 4, and the other set (line B) cooled from day 4 onwards. Cells per ml. plotted on a logarithmic scale (vertical axis). The temperature ($^{\circ}\text{C}$, vertical axis) in each set of bottles is shown above. Time in days, horizontal axis.

indeed, seen in both the experiments described above (Figs. 9, 10), where the decline in growth rate and final cessation of growth is due to depletion of the nutrient supply. When supplied with fresh nutrients the cells resume exponential growth after a lag period of about 24 hr. (cf. Fig. 8). To what extent chemical conditions control the growth rate in nature, where (or when) nutrient concentrations are low, is unknown, though the rate of supply must be controlled by water turbulence (cf. Lund, 1947).

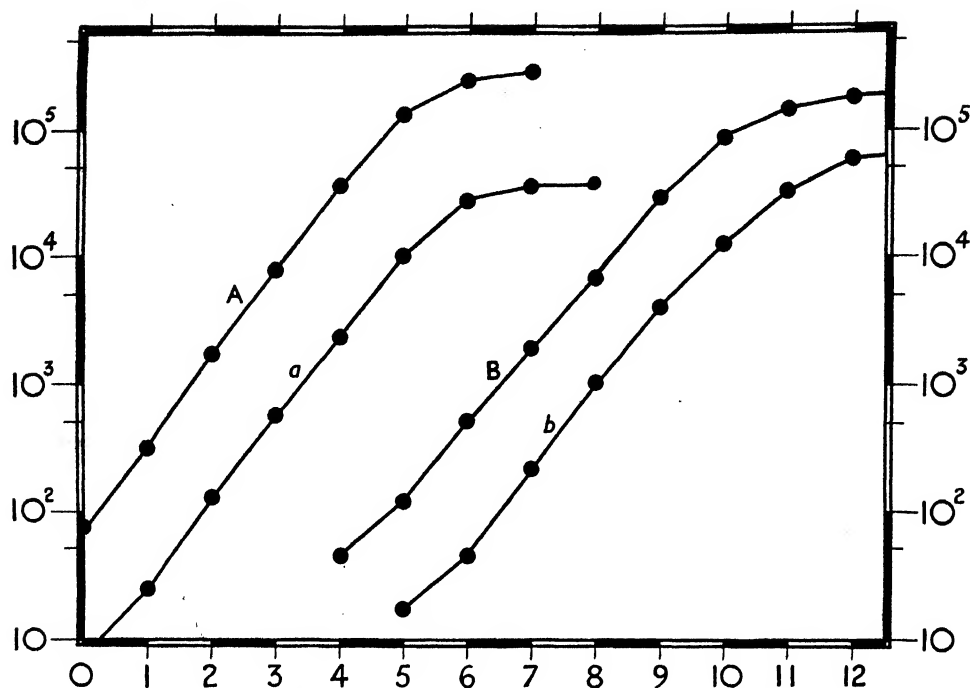


Fig. 11. Growth rate of *Asterionella* in relation to the concentration of salts in solution. Two experiments (A, a and B, b). The ratio of the amounts of silica in the solutions after sterilization varies from that originally present owing to the solution of the Pyrex glass produced by this process. Left-hand graphs: A, solution ten times (silica nine times) as concentrated as a. Right-hand graphs: B solution four times (silica three times) as concentrated as b. The two experiments were carried out in light from fluorescent lamps of somewhat different intensity and spectral composition.

(c) *An explanation of the apparently constant growth rate in nature*

Pearsall *et al.* (1946) and Storey (1942) define the logarithmic growth rate by the formula $\log N_t = \log N_0 + kt$, where N_t is the number at any time, N_0 the number originally, k the logarithmic growth rate and t the time interval. It does not seem to me that by applying this formula to data obtained from sampling a natural population they can bring evidence suggesting 'that standing crops of algae tend to maintain a constant growth rate during their period of growth' from which springs the further suggestion 'that this represents an integration of the environmental factors which operate at an early stage of the growth cycle' (Pearsall *et al.* 1946, p. 49). What they actually measured was the rate of increase of the population at the collecting station. This population at any one time is not composed solely of the descendants of the population examined the previous time. For example, under isothermal conditions, the cells are being moved vertically as well as horizontally, while under stratified conditions, though vertical movements are limited, considerable horizontal movements may occur. Such seiches (Wedderburn & Young, 1915; see Busse, 1937, for relation to algal numbers) lead to the greatest changes in numbers near ends of the lake basin (i.e. of the oscillation). Since the numbers of *Asterionella* in the surface layers of the lakes examined are much the same over most of the lake area the amount of horizontal movement at a central station will not yield marked numerical differences despite the changing positions of the cells in them. The 'growth rate', cf. Pearsall *et al.*

(1946), may or may not be synonymous with the actual growth rate of the cells. In cultures in enclosed vessels the same population and its descendants are sampled. In the lake the population increase observed between any two times of collection is the difference between the gain in numbers of cells due to their rate of growth and the loss due to the removal or death of cells (e.g. to outflow or the bottom; by parasitism—Canter & Lund, 1948). It is impossible to observe small changes in growth rate since 'a plankton collection taken from any well-mixed part of a lake is itself a true sample, and hence the count made from it is subject to statistical "error"' (Ricker, 1937, p. 84). Taking a count of 100 colonies and 0.95 confidence coefficient (Ricker, 1937, p. 74) the upper and lower limits are 82 and 122 colonies respectively. Since the number of cells per colony commonly varies between 6 and 7 the count, which is expressed in cells, may vary between 492 and 732, or 574 and 854, which is equivalent to a change in numbers of about 50%.* Moreover, one of every twenty such counts may be expected to be outside these limits. Since the reduction in the confidence limits varies as the square root of the number of colonies counted, the time involved in reducing such limits appreciably is prohibitive. Under isothermal conditions, such as occur in early spring, it is quite possible for the rate of population increase to be more or less constant for a time even in the absence of such complicating factors as floods, nutrient depletion or parasitism. The length of time any one cell spends at any depth depends on chance and turbulent water movements. It is reasonable to assume that if the growth rate of all the cells suspended in the lake water could be plotted graphically, a normal frequency distribution curve would be obtained. Moreover, the increase in temperature is slow since the whole body of water is concerned. Indeed, the temperature range from the beginning to the end of the spring-growth period, even in the surface layers, is only of the order of 10° C. (note the difference in growth rate in Fig. 10). Similarly, the effect of light increases are damped by the fact that the photic zone, as found by the experiments described on pp. 408–9 is only from 0 to 5 or 10 m. (i.e. about one-sixth to one-third the mean depth in the case of Windermere north basin), and the majority of the cells are only in it for a short time.

It is further probable from experiments on algae (e.g. Juday & Schomer, 1935; Schomer & Juday, 1935; Loose, Pearsall & Willis, 1934; see also Miller, 1938) that a limit will be reached, at least in the upper layers of the water, above which the rate of photosynthesis will not increase regularly with increasing light. Very high light intensities may be detrimental. Such light intensities are only likely for a period during fine days, and it is not suggested that the growth of the population, in, for example, the 0–5 m. water column, is likely to be stopped. Fig. 7 shows that cultures of *Asterionella* in bottles suspended in Windermere produced the largest growths during periods with the highest total illumination. It is suggested that the growth rate will not alter regularly throughout the wide range of light intensity occurring under natural conditions. These factors also operate in the epilimnion once stratification has set in with the added loss of cells to the thermocline and hypolimnion. This may be compared with the loss to the bottom of the lake under isothermal conditions. Since the thermocline zone presents a much greater surface area than the bottom, losses to the former may be expected to be correspondingly greater than to the latter. Further, stratification, in these lakes, usually sets in towards the end of the growth period when depletion of silica and possibly other unknown nutrients is becoming marked. Rate of supply will thus be reduced and this may well reduce the rate of growth

* This does not allow for the cell per colony distribution which may even increase the limits.

in such a dilute salt solution (see p. 411). What may be expected is a noticeable increase in growth rate and so of population in the absence of increased losses (e.g. due to floods, parasitism) if there is a relatively sharp onset of stratification before nutrient depletion begins to be serious. This can be seen to occur. It was particularly marked in Windermere north basin in 1946 when an early period of quiet, hot and sunny weather led to a temporary stratification. The cells collected in a 0–5 m. water column by means of the tube method (p. 390) had then for a period been largely confined to the photic zone. Between 27 March and 3 April the population increase rate was doubled, there being the equivalent of about $3\frac{1}{2}$ divisions in a week (Fig. 1, X), an unusually high rate for the lakes concerned. In the relatively shallow Esthwaite Water and Blelham Tarn, in the absence of floods and parasitism (Canter & Lund, 1948), the population increases through all but the shortest days of winter. The rate is, however, slower than in spring though it may be as fast in early autumn. These changes are explicable on the basis of the effect of decreasing light and temperature. The opposing series of changes that might be expected from early spring to the period of the highest light and temperature in midsummer cannot be clearly observed because growth is so great before this that nutrients have limited or ended the growth period. The data of Pearsall *et al.* (1946) and Storey (1942) do not, therefore, necessarily show that the growth rate of *Asterionella* is more or less constant, despite changes in light and temperature, since this may be expected within certain limits from the relatively slow rate of change in so large a volume of water as a lake, the changes in the effects produced by these factors at varying levels (e.g. light, p. 409) and the regularity or irregularity of the losses due to factors such as floods, parasitism, etc. Moreover, marked environmental changes can sometimes be correlated with changes in the rate of increase (or decrease) of a population in the lake. Laboratory experiments (pp. 409–410) show that such changes can be induced in cultures by alterations in the light intensity or temperature within a day or two irrespective of whether growth was fast or slow before the alteration in light (Fig. 9). My view is, therefore, that the growth rate of *Asterionella* is directly related to the immediate changes in the environment.

VII. DISCUSSION

The production of large maxima of *Asterionella* appeared at times to Whipple (1894),* Whipple & Jackson (1899) and Wesenberg-Lund (1908) to be too rapid to be explained by the growth of the cells in the open water alone, but must consist partly of material raised from the bottom. Whipple (1894) and Whipple & Jackson (1899) observed that periods of active growth are related to the 'times of water circulation' and believed that, during periods of 'stagnation' (stratification), the cells quickly sink through the thermocline, some forming resting spores which are later raised to the surface. Wesenberg-Lund (1908, pp. 50–51) agrees. He doubts whether there are any purely limnetic diatoms, pointing to the littoral region as a possible source of cells which, on arrival at the surface, are carried out into the lake by waves (Wesenberg-Lund, 1908, p. 54). He does, however, state (1908, p. 15) 'that we know nothing certain' concerning this. Sprenger's (1925) views are the same, while Chu (1945) states that most, if not all, important plankton algae originate from inflowing waters or the littoral zone, particularly muddy bays and reed-swamps where conditions are suitable for their development. West & West (1909), who studied the plankton of Windermere, disagreed with Wesenberg-Lund. Godward (1937), from a study

* I am indebted to Prof. G. W. Prescott for photo copies of Whipple's papers.

of the littoral attached algae of Windermere, considered *Asterionella* to be a purely planktonic diatom. She states that the material on the bottom usually consists of dissociated colonies.

In the present investigation no resting spores have been observed and, of the many workers who have examined plankton rich in *Asterionella*, only Whipple & Jackson have figured (1899, pl. 1, fig. 5, *a-f*) such possible spores. These figures strongly suggest that the 'spores' were actually the more or less decomposed remnants of the chromatophores.

Whipple (1894) stated that 'the increase of diatoms takes place substantially in accordance with the laws of geometrical progression' but, from his views detailed above, it is doubtful whether he fully grasped the implications of this statement. If in a dense population two or three divisions take place quickly, the result is a vast increase in numbers in a short space of time. Whipple (1894, see also Whipple & Jackson, 1899) found the increase in numbers during vigorous growth to be commonly about '50% per week', which is considerably less than those observed in the English Lake District, and about one-quarter that recorded for London Reservoirs (Pearsall *et al.* 1946). In the lakes here investigated (Figs. 1-4, 6) the increase in numbers is so regular that no hypothesis concerning outside sources of enrichment seems necessary to explain it. Indeed, extensive sampling of the deposits (pp. 395-8), the plankton of bays and of inflowing water (pp. 398-402) of the lakes concerned has led to the view that the changes in population density in the open water are the result of the action of the environment on the cells there suspended.

The suggestion by Storey* (1943, 1944; see also Pearsall *et al.* 1946; Harvey, 1945, pp. 129-30; Hutchinson, 1944, p. 24) that, after the spring maximum of *Asterionella*, the majority of the cells become physiologically dormant and incapable of growing under the most favourable cultural conditions has been considered on pp. 402-5 and an alternative view taken, namely, that, at the most, only the minority of the cells pass into such a state.

Chu (1943, pp. 140-2; 1945) found that cultures showed signs of phosphorus deficiency at phosphate concentrations lower than 0.045 mg. per litre, and no growth took place below 0.01 mg. per litre. Gardiner (1941) found a correlation between the changes in the phosphate concentration of the water and development of *Asterionella*, and other diatoms, in reservoirs where phosphate was of the order of 100 times the concentration in the lakes here studied. During the four years I have studied the four bodies of water here considered, the phosphate concentration has never exceeded 0.005 mg. P per litre and is usually about 0.001 mg. P per litre (cf. Chu, 1945; Lund, 1947). Chu (1943) observed nitrate deficiency in cultures with less than 0.5 mg. N per litre, a concentration also above the maximum in Windermere, north basin, which produces a spring maximum as do Esthwaite Water and Blelham Tarn in which such concentrations do sometimes occur. Chu (1945) inoculated *Asterionella* colonies into filtered Windermere water and obtained no significant growth, although the cells came from healthy cultures and might be expected to contain plentiful reserves. Occasionally two and very rarely three divisions occurred in the Windermere water, and these he considers to be due to the utilization of these reserves rather than any nutrients in the lake water. The possible reason for the lack of agreement between these experimental findings and observations on the cell production in the lakes is discussed in Lund (1947). Moreover, Rodhe (1948, p. 78 *et seq.*), in synthetic solutions, obtained similar results to Chu for the phosphate requirement of *Asterionella* but, in lake water, he found the phosphate requirement of the cells bore no resemblance to that reported by Chu. Since

* Miss J. Storey (Mrs David) has kindly put all her data at my disposal.

very low concentrations of phosphate sufficed in lake water he assumes that it contains a factor absent in his and Chu's culture solutions. Though repeated experiments confirmed his findings, in general, it was very difficult to obtain completely concordant results using single colony inoculations from the same clone. It appears to him that the physiological condition of the cell is also very important. This last finding is similar to that of Storey (1943, 1944). In her case, at least, one of the possible reasons for the failure of the single colony isolations after the time of the *Asterionella* maximum in Windermere is that most of the colonies are then dead or dying. In general, single cell or colony inoculations from natural to cultural environments is not easy to carry out without damage to the cells concerned. Chu (1945) holds that 'floods, water-currents, winds and wave-action are the main immediate factors affecting the distribution of plankton algae in the open water'. The sparse nutrients in the open water are unable to support the growth of *Asterionella*, multiplication being limited by the amounts stored in the cells. Sooner or later they sink to the bottom. Moreover, he found (see p. 415) the cells cannot store enough nutrients to permit more than, at the most, three divisions, when placed in a medium deficient in them. He believes, therefore, the increase in cell numbers in the plankton and duration of the maximum to be mainly related to replenishment from the littoral. Chu (1945, p. 23) summarizes his views by saying that, if the above be so, then: 'a state of non-correlation between the increase and decrease of a phytoplankton on the one hand, and the chemical and some other factors such as temperature and sunshine on the other, is not unexpected in a lake containing a poor supply of nutrients such as Windermere'. The results of the present investigation are not in accordance with his views, but suggest that the growth of *Asterionella* occurs in the open water, is directly related to environmental changes occurring there and that, at the times concerned, there is a sufficiency of nutrients to permit the production of large maxima (5×10^6 to 10^7 cells per litre).

VIII. SUMMARY

Two possible views concerning the origin and nature of the cells producing the seasonal maxima of *Asterionella* in the plankton of certain lakes have been investigated.

Live cells of *Asterionella* were always present in the open water (pp. 394-5) and some, at least, able to grow if sufficient nutrients and light were available (pp. 402-5).

The littoral and profundal deposits receive cells from the plankton, but there is no evidence that they act as centres of production of cells later carried out into the plankton (pp. 395-401). Relatively large populations in the plankton of some sheltered bays of Windermere north basin, due to inflow of cells from other lakes, may precede those in the open water which form the spring-growth period. It does not appear that these are the 'inoculum' for the production of the maximum in the open water (p. 398).

Two of the lakes from which cells pass into Windermere show a similar periodicity, though one (Esthwaite Water) receives very little enrichment from its drainage area, and the other (Blelham Tarn) receives none (pp. 401-2). It is suggested that supply from outside sources is not necessary for the production of maxima in Windermere and this view is supported by laboratory experiments (pp. 404-5).

No morphological or physiological resting stages have been observed.

The growth rate of *Asterionella* in culture varies immediately, or within a very short period, with physical alterations in the environment irrespective of the growth rate in the inoculum used for the experiment concerned (pp. 405-11). It does not vary in relation to

the nutrient concentration of the medium so long as this is in excess of immediate needs and is not lethal.

The term 'growth rate' for the increase in the population in a lake is a misnomer (p. 412), and an alternative explanation of the apparently approximately constant rate of increase of the population in nature is given.

In the author's view the data for the lakes concerned is consistent with hypothesis (b) (p. 390), but not with hypothesis (a).

The author is greatly indebted to his colleagues, in particular to Mr H. C. Gilson, director of the Freshwater Biological Association and Dr C. H. Mortimer for advice and criticism, to Miss B. M. Knudson, Mr F. J. Mackereth and Mr D. Gawen for assistance.

IX. APPENDIX

Descriptive list of sampling stations

References to the Ordnance Survey (1947) maps covering the localities concerned are given in brackets after their names. For example, O.S. 35/30 = Ordnance Survey, Sheet 35/30, while O.S. 376015 is the national grid reference for the sheet concerned. The depth of the deposit below the water surface when the lake level coincides with the ordnance datum of 129.00 ft. (Ordnance Survey, 1947) is given in brackets after its description. Only the common rooted plants, where present, are mentioned and their abundance indicated by the symbols: a., abundant; f., frequent; o., occasional; r., rare; v.r., very rare. For further details concerning most of the shallow plant-bearing deposits see Misra (1938), and of the deeper deposits see Pennington (1943).

A. WINDERMERE, NORTH BASIN (O.S. 35/30).

1. *Sawpit Bay* (O.S. 376015), at the following distances from a fixed point of the shore:
 - (a) 12 m. On the wave-cut terrace; boulders and coarse silt (1 m.); *Littorella uniflora* (L.) Aschers (f.), *Isoetes lacustris* L. (r.).
 - (b) 18 m. At the base of the wave-cut terrace; gravel and silt (2 m.); *Littorella uniflora* (f.), *Isoetes lacustris* (f.).
 - (c) 48 m. Bare mud; occasional patches of clay (3.5 m.).
 - (d) 80 m. Bare mud (5.5 m.).
 - (e) Various distances farther from shore; semi-liquid ooze (10–40 m.); occasional observations.
2. *Low Wray Bay* (O.S. 376013). Fine black mud (3.5 m.); *Potamogeton praelongus* Wulf. (f.), *P. perfoliatus* L. (o.); occasional observations.
3. *Sandy Wyke Bay* (O.S. 377024):
 - (a) Sand (0.5 m.), *Phragmites communis* Trin. (a.).
 - (b) Sand (0.75 m.), *Phragmites communis* (a.); *Lobelia dortmanna* L. (f.).
 - (c) Fine silt (2 m.), *Littorella uniflora* (a.).
4. *Pull Wyke Bay* (O.S. 364021–366022):
 - (a) Centre; occasional plankton samples.
 - (b) Pull Wyke Swan; brown peaty mud (0.75 m.); *Scirpus lacustris* L. (f.), *Equisetum fluviatile* L. (f.).
 - (c) Pull Wyke Swan; brown mud (0.75 m.); *Sparganium minimum* (Hartm.) Fr. (a.), *Littorella uniflora* (v.r.); much bare mud ('sterile region' of Misra, 1938, p. 440).
 - (d) Pull Wyke Swan; peaty (0.25 m.); *Carex rostrata* Stokes (f.), *C. elata* A11 (f.), *C. vesicaria* L. (r.), *Phragmites communis* (o.).
 - (e) Near mouth of Pull Beck; peaty mud (0.5 m.); *Scirpus lacustris* (a.), *Phragmites communis* (r.); occasional observations.

- (f) Near mouth of Pull Beck; brown mud (1.25 m.); *Sparganium minimum* (f.), *Potamogeton alpinus* Balb. (f.), *Elodea canadensis* Michx (r.); some bare (sterile) mud.
- (g) Near Pull Beck; brown mud (1 m.); *Potamogeton alpinus* (a.); occasional observations.
5. Bee Bay (O.S. 371019). Peaty (0.25 m.); *Carex lasiocarpa* Ehrh. (a.).
6. Congo Bay (O.S. 370019). Plankton samples.
7. Gale Naze Bay (O.S. 370030). Plankton samples.
8. Central Buoy (O.S. 383008). Semi-liquid ooze (80 m.); standard plankton sampling place; occasional observations.
- B. BLELHAM TARN (O.S. 35/30).
1. Buoy. (O.S. 366006). Standard plankton sampling place; semi-liquid ooze, brown or black according to presence or absence of free oxygen (12 m.); occasional observations.
2. West End (O.S. 364003). Deepest point; as B1 (15 m.).
3. Near boathouse (O.S. 368005). Peaty mud (0.75 m.); *Typha angustifolia* L. (a.).
4. Near outflow (O.S. 368006). Peaty mud (0.5 m.); *Phragmites communis* (a.).
5. Near mouth of Fish Pond Beck (O.S. 365005). Peaty (0.25 m.); *Carex elata* (f.), *C. rostrata* (a.).
- C. BLELHAM FISH POND. (O.S. 35/30: 363007). Plankton samples.
- D. BRATHAY-ROTHAY CONFLUENCE (RIVER BIRDHOUSE) (O.S. 35/30: 370035). Below Rothay bridge; occasional plankton samples.
- E. ESTHWAITE WATER (O.S. 34/39). Buoy at north end. (O.S. 358969); standard plankton sampling place; deposit (13–15 m.) as B1; occasional observations.
- F. PRIEST'S POT (O.S. 34/39: 358978). Occasional plankton samples.
- G. BLACK BECK (O.S. 34/39: 358977). Below mouth of inflow channel from Priest's Pot; occasional plankton samples.
- H. CUNSEY BECK (O.S. 34/39). At various points between outflow of Esthwaite Water and (O.S. 367952) inflow into Windermere, south basin (O.S. 386935); occasional plankton samples.

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REVIEWS

Nicholas Polunin. *Botany of the Canadian Eastern Arctic. Part II. Thallophyta and Bryophyta.* National Museum of Canada Bulletin no. 97 (Biological series no. 26). Pp. v+573, 18 plates, 5 figures in the text and folding map. Canada Department of Mines and Resources, Mines and Geology Branch. 1947. Price \$1.

Unlike Part I, Part II of the *Botany of the Canadian Eastern Arctic* is a co-operative work which Prof. Polunin has edited, and to which he himself contributes only the introduction, the article on 'Hepaticae', and a conclusion. The other contributors are Roy M. Whelden (Algae), Gunnar Seidenfaden (Marine Phytoplankton), Robert Ross (Fresh-water Diatomeae), David H. Linder (Fungi), Bernt Lynge (Lichenes) and W. C. Steere (Musci). Though Dr Polunin has compiled the article on Hepaticae, the identifications are by others. The volume bears the non-committal title 'Botany' which might lead one to expect some general treatment of the flora, including perhaps its ecology; it is, however, essentially a systematic list, giving for each species the records of its occurrence throughout the region covered by the flora—i.e. the coastal regions of Hudson Bay and Quebec north of latitude 60°, and most of the islands from Hudson Bay north to Ellesmere Island. There is also a note on the general distribution of each species; there are sometimes additional notes, but these usually refer either to geographical distribution or to systematic problems; there is very rarely any information on the biology or habitat of the species except for the fungi; indeed, Linder's article is noteworthy both for the frequency of notes of this kind and for its keys and diagnoses. The introductions both to the work as a whole and to the separate articles are essentially historical accounts of the collecting of the group in question in the area. The articles on marine phytoplankton and on mosses have brief but useful concluding sections in which the authors summarize some of the salient features of the flora, but Polunin's conclusion to the volume as a whole consists only of a tabular statement of the distribution of the species by districts within the region covered by the flora. It would doubtless be premature to expect much more at this stage in a volume which, despite its title, clearly claims to be nothing more than a floristic list of a very imperfectly worked area, yet some indication of how this flora compared with other known arctic floras would have been welcome.

The compilers of these careful and critical lists have obviously performed a very useful task for specialists in the groups concerned, and one hopes that by providing future botanists who may visit the Canadian arctic with an authoritative list of the species already known, it will stimulate them to more adequate collecting of the cryptogams, and form the basis for a much fuller knowledge of the flora. For others, e.g. students of geographical distribution, the volume may provide a useful mine of raw material.

Throughout, Polunin's own collections contribute an important and sometimes an overwhelming proportion of the records; indeed, the accounts of the Algae and the Fungi include only his records, and it does not appear in these instances that the omission of earlier work is any serious detriment; the volume as a whole is solid testimony to Polunin's zeal in collecting during his travels in this little-worked region.

E. W. JONES

McDougall, W. B. *Plant Ecology.* 6 × 9½ in. Pp. 234. 4th edition, thoroughly revised, with 118 illustrations. 1949. London: Henry Kimpton. 20s.

The earlier texts on plant ecology reflected the outlook of the post-Darwinian period; plant communities could be 'explained' in terms of causal factors. It was logical, therefore, to begin with causes. Modern texts do not show the same optimism, for they begin with some account of what a plant community is and regard it as influenced, but not caused, by environmental factors. In this book the account of what a plant community is, is dealt with in a series of chapters describing the social and nutritive relations between plants, classified according to the author's well-known but not widely accepted scheme. Subsequent chapters deal with habitat factors; plant communities, their structure and classification, their distribution in the United States, and plant succession. Despite this approach one is left with the

impression that the book has attempted either too little or too much: there is much useful information in it, but the facts are not so well knit into the pattern as they might be.

The second comment which a reading of this book suggests is that much of the information contained in the first three chapters, entitled, 'The Ecology of Roots, The Ecology of Stems, and The Ecology of Leaves', is the kind of information commonly found in elementary texts in general botany and assumed to be known by the beginner in ecology. Whether ecology is best approached as a subject *per se* or as one superposed on previously obtained morphological and physiological knowledge is an open question, but it is doubtful if the botanical information provided is the best with which to introduce ecology. Would it not be better to begin with the plant as a living whole? After all, there are many successful applied ecologists who know nothing of the 'inside' of a plant.

One might have expected that an American text-book in ecology, with American plants and plant communities cited as examples, would be so foreign to the English reader as to be useless. To the beginner such citations present obvious difficulties: but they would do so were the examples English or European. To anyone past the initial stage such a book stimulates the reader to match the American with European examples. The parallelism in presentation and in essential principles is an outcome of the common heritage of ecological thought exercised on material so essentially the same on each side of the Atlantic that it makes one wonder whether the species has that degree of significance in plant communities and in their diagnosis and classification which European ecologists attach to it.

The book is profusely and appropriately illustrated. The high standard of production is somewhat marred by the number of misprints, including one in a chapter- and page-heading.

A. S. WATT

The Citrus Industry. Vol. II. *The Production of the Crop*. Edited by L. D. BATCHELOR and H. J. WEBBER. $9\frac{1}{2} \times 6\frac{1}{2}$ in. Pp. 933, with 297 figures (mostly photographic), including 12 colour plates. University of California Press. 1948. Price 55s.

This is part of an encyclopaedic work on the citrus industry, in which various problems of crop production are discussed each by a specialist in his particular topic. The general editors, and many of the contributors, are, or were, at the California Citrus Experiment Station or related institutions, so it represents a sum of experience hardly to be matched elsewhere. The book aims, however, by taking other citrus-growing areas also into consideration, to avoid too parochial an outlook; and the authors attempt, on the whole with success, not simply to cater for the needs of the purely practical reader, but to explain at least the elements of the scientific principles involved.

Written primarily from the point of view of the agriculturalist, some parts of this volume (such as chapters on nursery methods, rootstocks, pruning, and rodents) are of no special interest to the ecologist. Unfortunately, the long chapter on fungus and virus diseases is treated in such a way that it too must be included in this category. On the other hand, some of the chapters make stimulating reading, for the economic urge to push the growth of citrus into areas for which it is not naturally suitable brings certain of its ecological properties into prominence, and the necessity of providing for these weaknesses has led to their study in unusual detail. The two salient characters, which receive much attention in the book, are the sensitiveness to frost, and the requirement of the root system for a high degree of aeration.

Of course, other plants are damaged by frost too, but citrus being rather sensitive and grown near to or even beyond its temperature limits, the conditions causing damage and the circumstances which give rise to these conditions—such things as frost pools and thermal belts—are unusually well described. The account should be a healthy corrective to any tendency to regard a climatic limit as definable by isotherms, for it tells how a rare frost in a generally mild climate is much more damaging than regular cool temperatures, since it catches the trees when they are not in a relatively resistant dormant state: this dormancy resistance, it is remarked, is influenced by the mineral nutrition of the plant. Watt recently stressed the potential importance of rare unfavourable seasons, in connexion with the climatic determination of alpine vegetation, the interpretation of which would be much easier if we possessed for the alpine species the same detailed knowledge of their climatic reactions as we have for citrus. With the latter, not merely is it possible, for example, to define temperatures which successively damage flowers,

fruit, leaves, twigs and branches—but even to recognize conditions which stimulate vegetative growth while diminishing fruiting. The incidental observation that, even in so loose a plant as a citrus bush, the central portions may be several degrees warmer than the exterior during cold weather, lends point to Raunkaier's interpretation of the tussock form of alpine as a protection against cold as well as loss of water.

The high degree of aeration required by the roots of citrus is linked with the water relations of the soil—soils which are waterlogged, or may become so, are not suitable. Proper activity of the roots is made the more necessary by the rather exacting demands of the citrus plant for water, for not only is it evergreen, but, as the fruit takes a year to mature, the tree carries fruit always, and thus the results of transient water shortage at whatever season are likely to be serious. Irrigation therefore is frequently essential; and where not essential, it almost always increases the quantity of the crop, often enough to make irrigation pay. The problems of irrigation are shown to be least on soils with high water-binding capacity, and most acute on shallow poorly drained soils, or soils which pack readily and become impermeable. In such situations it may help to interplant the citrus trees with a cover crop which improves the tilth and aeration of the soil. A contributory effect of the cover crop is supposed to be a reduction of water loss by the citrus, through a general increase in the humidity of the air, but the book points out that the supposed gain may be offset by the competition of the cover crop with the citrus for the water supplied. From the increasing practice of 'clean' cultivation, in which the soil is kept bare of vegetation by oil spraying, one would infer that it is doubtful if anything is gained by allowing even so partial an approach to a natural vegetational structure.

Besides subjects wholly botanical there are in this volume a number of general matters illustrating useful ecological principles. For example, there is the relation of climate and fruiting season to the attacks of the Mediterranean fruit fly, which does little damage in Spain because the fruiting period (winter) is too cold, but which is a serious nuisance in the Eastern Mediterranean in preventing the extension of the citrus season into the warmer months of spring. In the same sphere are descriptions of the relations between insects parasitic on citrus, such as scale-insects and flies, and fungi parasitic on those insects—the attack of the fungi is so much enhanced in humid air that the insect pests may be practically eliminated by a natural biological control in relatively damp citrus areas like the 'hammock' lands of the Florida swamps, and in Central and South America. Such complex relations doubtless exist in many other connexions, but they are seldom so well understood. A chapter on quarantine regulations rounds off the comprehensive treatment of the numerous pests.

Representing, as it does, a mass of information not otherwise easily available, this volume is indispensable to anyone interested in citrus, and valuable to the general reader; and it is fittingly dedicated to the memory of H. J. Webber, its senior editor. It is of a size and a standard of production commensurate with its function; there is, for instance, a good series of colour photographs of diseases due to fungi and mineral deficiencies. The price is reasonable.

M. INGRAM

Trochain, J. (1940). 'Contribution à l'Étude de la Végétation de Sénégal.' Pp. 483 + 30 plates and 30 figures in the text. *Mém. de l'Inst. franc. d'Afrique Noire*, No. 2. Paris: Librairie Larose.

This important study of the vegetation of Senegal is not yet as widely known in this country as it deserves to be; it may therefore be not inappropriate to review it here, even nine years after its publication.

A brief summary of the contents will give some idea of the scope and thoroughness of the work. The brief introduction is followed by an account of the environmental factors, including a detailed description of the climate and its seasonal changes; information is also given about the geology and soils. Chapter 2 deals with the methods used; chapter 3 with the phytogeographical regions of West Africa and with the concept of the climax as applied to tropical African vegetation. Chapters 4–9 inclusive, which occupy the greater part of the book, are a systematic account of the plant communities of Senegal, divided first of all into those of aquatic and partly aquatic habitats (including mangrove and beach vegetation), and those determined mainly by the climate. The latter are subdivided into the communities of the *Domaine Sahélien*, the *Domaine Soudanien*, the *Domaine Guinéen* and the *Domaine Subguinéen*. The work

concludes with a list of the species observed during the author's travels, a résumé and a copious bibliography, but, alas, not with an adequate index.

Because of its accessibility from western Europe, Senegal has been longer known to botanists than any other part of tropical Africa. From 1749 to 1753, when Michel Adanson collected 500 species, to our own times, the flora has been repeatedly studied and M. Trochain justly claims that it is now better known than that of any other African colony. On the other hand, little attention had been given to the plant geography or ecology of Senegal until in 1930-1 and 1933-4 the author undertook two journeys, travelling, he says, by train, car, canoe, aeroplane and on horseback, as well as on his own feet. These journeys enabled him to study the plant communities in all their seasonal aspects, which added greatly to the value of his survey, since in Senegal, as throughout the Sahelian and Sudanian regions of Africa, there is an extreme contrast between the luxuriant greenness of the vegetation during the rains and its desiccated condition during the dry season.

Senegal is a country which at first sight does not seem inviting for ecological researches. There are no hills higher than 200 m. and bold topographical features of all kinds are lacking. The changes in the aspect of the vegetation from place to place, though numerous and rapid, are neither conspicuous nor easy to interpret. There is a considerable population, and all the plant communities have been drastically modified by cultivation, grazing or burning. Not a square inch of the surface, according to M. Trochain, escapes the annually recurring bush fires. There are thus no climatic climaxes and to reconstruct the original plant covering it is necessary to copy the methods of the archaeologists.

The flora is small—the total number of species of flowering plants is estimated at 1100—but is of interest because Senegal lies only slightly to the south of the boundary between the Holarctic and Palaeotropical biological regions. Thus, among a majority of tropical African species, many of which here reach their northern limit, a few European plants are found, e.g. *Scirpus maritimus* and *Suaeda fruticosa*. As might be expected from the geographical position, some of the plant communities are much impoverished; the mangrove, for instance, consists mainly of two species, *Rhizophora racemosa* and *Avicennia nitida*.

Since most of the book consists of a systematic description of the vegetation of an area which is not self-contained, but consists of a cross-section of zones of vegetation extending across the entire width of Africa, we cannot expect to find here startlingly novel conclusions nor much which readily lends itself to summarization. What will perhaps be of most interest to readers of the *Journal of Ecology* are the author's views on the history of the vegetation and the climatic oscillations in the area during the Quaternary. He believes that there have been four phases of climate: (1) a humid period (early Palaeolithic?), during which the rivers of the Sahara were flowing. Senegal was then covered with a dense forest. No relict stands of this forest remain as such, but in a very limited area near the coast, thanks to a locally favourable climate, there is an aggregation of species whose main area of distribution is in the *forêt dense* far to the south of Senegal and which are probably to be regarded as forest relicts, e.g. *Xylopia ferruginea*, *Anthocleista frezoulsii*. These species occur scattered through thorny savanna, etc., and are in some places associated with oil palms. (2) A dry period during which *carapaces* of laterite formed in the subsoil and extensive dunes were built up in the western part of the country. At this time the forest retreated, probably maintaining itself on the borders of the coastal rivers and around fresh-water lagoons. (3) A second humid period, certainly Neolithic, during which the existing savanna woodland or *savane forestière* extended northwards, leaving relicts behind in (4) the present relatively dry period. The author considers the present climate to be stable, and agrees with Aubréville and others that the apparent desiccation which is taking place to-day is due to bush fires, deforestation, etc., and not to a secular climatic change. Records of rainfall have been kept at Saint-Louis since 1830 and give no evidence for any progressive diminution of rainfall.

The book is lavishly produced and well illustrated. One could perhaps wish that the style were somewhat more condensed and that less space were devoted to subjects such as the nomenclature of the vegetation zones which have been discussed at length by nearly all previous writers on the vegetation of French West Africa, but M. Trochain has certainly provided a mine of useful information which will be indispensable to all ecologists concerned with the Sahelian and Sudanian zones of Africa.

Grønlie, A. M. 'The Ornithocoprophilous Vegetation of the Bird Cliffs of Røst in the Lofoten Islands, Northern Norway.' *Nytt Magazin for Naturvidenskapene*, 86. Oslo, 1948.

The vegetation of the Lofoten Islands has been the subject of some investigation in the past, but one aspect, the vegetation of the bird cliffs, has not been described before in detail. This paper is an analysis of the plant associations which occur under conditions of heavy manuring by such species as Puffins (*Fratercula arctica*), Kittiwakes (*Rissa tridactyla*), Razorbills (*Alca torda*) and Guillemots (*Uria aalge*).

The islands of the Røst group have a very uniform flora, poor in species. Five main communities are recognized: (a) grass meadows, (b) meadows of large perennials, (c) nitrophilous communities of annuals, (d) cliff vegetation, (e) Puffin holes. (b), (c) and (e) are only described briefly and the main part of the paper is taken up with an analysis of (a) and (d).

(a) *Grass meadows*. Three types of grassland occur, dominated respectively by: (1) *Festuca rubra*, (2) *Festuca* and *Agrostis tenuis*, (3) *Festuca*, *Agrostis* and *Anthoxanthum odoratum*. The flora is analysed by data from a large number of quadrats. Soil profiles, all of the brown earth type, are described, and from several stations soil samples have been analysed for pH, loss on ignition, water content, calcium, phosphorus, nitrate and ammonia contents.

(1) The purest type of *Festuca rubra* meadow, in which the plants are usually sterile, presumably by reason of the low C/N ratio, occurs on slopes where Puffins nest and where, as a result, manuring is considerable and direct. The chief species are *F. rubra* and *Stellaria media*.

(2) *Festuca-Agrostis* grassland occurs on slopes devoid of Puffin burrows, but at the base of cliffs occupied by nesting Kittiwakes (*Rissa tridactyla*, etc.), where manuring is rather lower than in (1) and is indirect, resulting from the washing down of soluble compounds. It is characterized by *Festuca rubra*, *Agrostis tenuis*, *Poa pratensis*, *Stellaria media* and *Cerastium caespitosum*.

(3) The third type is found again on slopes, but away from numerous resting birds, and where as a result manuring is relatively slight. The species occurring there are *Festuca rubra*, *Agrostis tenuis*, *Anthoxanthum odoratum*, *Poa pratensis*, *Rhytiadelphus squarrosus*, *Rumex acetosa*, *Cerastium caespitosum*, *Stellaria media* and *Deschampsia caespitosa*.

The relation between these three associations and the degree of manuring is suggested by the locations in which they occur, and the analyses for nitrogen, nitrate and ammonia do show a decreasing concentration gradient from (1) to (3). It had been suggested previously that ammonia is chiefly responsible for determining the nature of nitrophilous vegetation, but the author puts forward the view that the gradient in total nitrogen and nitrate is equally important. The phosphorus contents show a gradient parallel to that in nitrogen, and the author agrees with earlier suggestions of Summerhayes and Elton, and Du Reitz, that phosphorus may also be a significant factor in determining the nature of ornithocoprophilous vegetation. In all cases the pH was much lower than had previously been associated with conditions of high manuring—between 4.7 and 3.9—and does not appear to be related to the manuring intensity. Thus apart from a drop from pH 5.95 to 4.95 from pure manure to the first *Stellaria-Cochlearia* colonists, the value is more or less constant, though with some irregular variation.

The above sequence was from Trenyken. On Vedøy a slightly different sequence, from the base of a bird cliff down a sloping meadow, was examined and showed: (1) an area devoid of plants where droppings accumulate, (2) *Stellaria media-Cochlearia officinalis* association, (3) *Festuca-Agrostis* grassland, (4) *Festuca-Agrostis-Anthoxanthum* association. The nitrogen and phosphorus contents of this series again show the same trends.

(b) *Cliff vegetation*, again markedly ornithocoprophilous in nature, includes such species as *Cochlearia officinalis*, *Melandrium rubrum*, *Festuca rubra*, *Rumex acetosa*, *Anthriscus sylvestris*, *Matricaria inodora*, *Silene maritima*, and *Stellaria media*. On large ledges *Galeopsis tetrahit* and *Angelica archangelica* occur. The lithophytic vegetation, made up almost entirely of lichens, is analysed in some detail. Species such as *Physcia caesia*, *Xanthoria candelaria*, *Lecanora leproscens*, *L. straminea*, *Caloplaca granulosa* and *Buellia conips* are highly ornithocoprophilous, while a *Ramalina siliquosa* association is rather less so. On the other hand, some species, e.g. *Parmelia saxatilis*, *Anaptychia fusca*, etc., are confined to zones

where manuring is much weaker, and the detrimental effect of heavy manuring upon such species is described.

There follows a detailed list of all the species of phanerogams, bryophytes, lichens and algae encountered, with a consideration both from the present and from other published data, of the more or less ornitho-coprophilous nature of each one. In conclusion, the relation which this vegetation bears to coprophilous associations in general is discussed, and attention is drawn to the very many resemblances which are seen to exist.

P. MARLER

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BRITISH ECOLOGICAL SOCIETY

SUMMER MEETING AT GLASGOW

2-6 AUGUST 1949

At the renewed invitation of Prof. J. Walton the Summer Meeting for 1949 was held at Glasgow, members being accommodated in Queen Margaret Hall, one of the Halls of Residence of the University. The Meeting opened at 8 p.m. on Tuesday, 2 August with a soirée in the Department of Zoology, by kind permission of Prof. C. M. Yonge, when about sixty members and guests enjoyed a most pleasant evening. Dr E. Conway opened by conveying apologies from Prof. Walton and Prof. Yonge, who were both away from Glasgow, and gave a warm welcome to the Society. Mr Hutchinson then outlined the programme for the Meeting, and after refreshment members inspected the numerous demonstrations. These involved a collection of British alpine plants grown, largely from seed, by Dr Dovaston; observations on the distribution and range of the midge *Culicoides impunctatus* by Mr D. S. Kettle, and other exhibits bearing closely on what was to be seen during the Meeting.

Wednesday, 3 August

On the following morning the party travelled in two buses to the Loch Lomond Freshwater Biological Station and Insect Field Station, in the grounds of Ross Dhu House, Loch Lomond. The staffs of the two Stations had arranged demonstrations and devoted themselves unsparingly to the task of explaining their work and answering members' questions. In the Freshwater Biological Station the main exhibit was of the work of Mr A. C. J. Weereboom, who had over a long period been collecting the bottom fauna at a series of stations with a Peterson grab. The studies of Miss R. M. Bullock on the biology and ecology of some species of Trichoptera (caddis-flies) were not on show since they had been seen at the soirée on the previous evening, but there was a demonstration of the salient hydrographical features of the Loch. In the Insect Field Station there was an interesting demonstration of two forms of the ant *Myrmica rubra*. In var. *microgyna* the queens have a head width of 0.88-1.06 mm., while in var. *macrogyna* the corresponding dimensions are 1.09-1.21 mm. In var. *microgyna* the fecundated queens are taken back into the nest, while in var. *macrogyna* the queens start new colonies after fecundation. Var. *microgyna* is found, in the neighbourhood of the Station, in farm hedges, walls and banks, while var. *macrogyna* occurs in newly made sites such as woodland clearings or patches of burnt heather. These differences in ecology are clearly related to the more rapid dissemination of var. *macrogyna*, analogous to the dispersal of seeds and fruits by wind and in contrast to the gradual 'vegetative' spread of var. *microgyna*. The precise genetic relationships of the two forms are not yet understood.

While most of the party left the Stations at about 11.30 a.m., a small number remained to see more of the work. This smaller party was taken out in the launch by Mr Hunter to inspect the hydrographical and hydrobiological gear used in the Loch, and in the afternoon had an opportunity to visit the site of Mr D. S. Kettle's work on the ecology of midges (*Culicoides* spp.). On posts erected at intervals there were tins covered with a sticky solution. These proved excellent traps for midges of both sexes and large numbers were caught. The numbers varied greatly from post to post, but the proportion caught by any one post remained fairly constant. By plotting 'lines of equal catch' and taking a projection to the centre of the circles so obtained Mr Kettle deduced where a search for larvae was likely to be profitable. Larvae were found eventually in a damp place where there was much *Sphagnum* and *Juncus effusus*. The species was *C. impunctatus*, the most important pest of man in Scotland. There are other species that bite, but the breeding places of all seem to be of the same type.

Meanwhile, the main party had proceeded by bus to the head of Loch Long, close to Arrochar, and had begun the ascent of Ben Narnain, neighbour of the well-known 'Cobbler' and reaching just over 3000 ft. in height. The route taken lay at first close to the Succoth Burn, much of it over gently sloping terraces dominated by *Molinia* and *Juncus* spp. By the main burn and its tributaries many arctic-alpine species were encountered at quite low altitudes—*Alchemilla alpina*, *Thalictrum alpinum*, *Saxifraga oppositifolia*,

S. aizoides, *Sedum rosea* and *Oxyria digyna*, all at heights below 1300 ft. At about 1750 ft. the now steeper slopes carried *Vaccinium myrtillus*, *Calluna*, *Deschampsia flexuosa*, *Festuca vivipara*, *Potentilla erecta*, *Alchemilla alpina*, *Luzula sylvatica*, and *Carex binervis* as the most prominent species, with *Lycopodium selago*, *L. clavatum* and *L. alpinum* as local associates. After a break for lunch the climb was resumed and just below 2000 ft. *Vaccinium uliginosum* and *Empetrum hermaphroditum* became plentiful on rocks. As often on mountains of Dalradian Schists there were local seepage zones of base-rich water characterized by such species as *Saxifraga aizoides*, *Juncus triglumis*, *Selaginella spinulosa*, *Carex dioica* and *Pinguicula vulgaris*. From the base of the great corrie the route now led up a long slope to the summit. At about 2800 ft. an exposed stony ridge showed an interesting open community with *Rhacomitrium lanuginosum* as the most widespread species, *Alchemilla alpina*, *Deschampsia flexuosa* and *Festuca vivipara* all fairly abundant, and with *Salix herbacea*, *Sibbaldia procumbens*, *Luzula spicata*, *Carex bigelowii* (rigida), *Empetrum hermaphroditum* and *Lycopodium selago* amongst the associated species. The summit plateau at about 3000 ft. had locally a more or less continuous carpet of *Rhacomitrium* with *Carex bigelowii*, *Vaccinium myrtillus*, *Deschampsia flexuosa* and *Festuca vivipara* as the only generally prominent associates, though *Nardus* was locally dominant in small hollows.

During the descent by a different route *Gnaphalium supinum*, *Epilobium alpinum*, *Saussurea alpina* and *Crytogramma crispa* were seen, and members had the satisfaction, by finding *Cornus suecica* just below the summit, of adding a new record to the list for the mountain. After a welcome tea at Arrochar the party was driven back to Glasgow having greatly enjoyed a most pleasant and interesting day.

Thursday, 4 August

The next day the party drove over Campsie Fells to Flanders Moss, west of Stirling. This extensive raised bog lies on the carse clays which in this neighbourhood carry very valuable crops of timothy grown for seed. The Moss was approached from the south and proved to have a rough surface considerably modified by burning. *Calluna* was abundant to dominant and there was a good deal of *Eriophorum vaginatum* and *Erica tetralix*. Sphagna were not as prominent as would be expected on an actively growing bog, but *Sphagnum papillosum*, *S. magellanicum* and *S. rubellum* were present in some quantity, and there was some *S. cuspidatum* in hollows. Of interest was the abundance of both *Andromeda* and *Oxycoccus*, so commonly seen on raised bogs with somewhat modified surface vegetation. Of still more interest was the small colony of *Ledum palustre*, consisting of about four plants, the two largest being about 1.5 m. in diameter. At this point the bog surface was dominated by *Calluna* with a great deal of *Polytrichum commune* and with numerous scattered young birches. *Ledum* has for long been known on Flanders Moss but its origin is obscure.

At the western margin of the Moss an old cut face showed many feet of *Sphagnum-Calluna-Eriophorum* peat with a well-marked Grenzhorizont about 3 ft. below the present surface. No detailed studies of stratigraphy or tree pollen have so far been undertaken, and it is to be hoped that we may soon learn more about this interesting area.

The party next drove on to the Ballochraggan Experimental Area of the West of Scotland Agricultural College, near Port of Menteith, Perthshire. Here Prof. K. W. Braid and his staff demonstrated their investigations into methods for the control of bracken. This area of 413 acres on Old Red Sandstone was heavily infested with bracken at the beginning of the experiments in 1942. Its vegetation was mapped in detail by Mr L. W. Poel so that the changes brought about by control methods could be accurately followed.

The bracken on the lower part of the area was cut twice in 1942 and 1943, and much of it twice also in 1944, with the Collins Junior Power Bracken Cutter. These cuttings so greatly reduced the growth that a single annual cutting has been adequate since 1945. There remains the problem of dealing with the bracken close to walls and fences and amongst shrubs and rocks. Sodium chlorate is effective but is much too expensive, and a far cheaper dust or spray is awaited.

Other control methods tried included the use of a flame-thrower and of scythes fitted with a device for smearing sodium chlorate on the cut surface, the former proving too heavy for easy portability and the latter rather doubtfully effective. Experiments with Methoxone and Agroxone were inconclusive, and

ploughing and reseeded was often disappointing. These careful investigations have shown the intractability of the bracken problem and point to regular cutting as still the most effective mode of control.

In the evening the Society were the guests of the University Court. They were received by the Principal of the University, Sir Hector Hetherington, in the Hunterian Museum, and then were shown the fine Hunterian Collection of pictures and manuscripts, the gift of Dr William Hunter (1742-90), brother of John Hunter. They saw also the interesting collection of Roman remains, chiefly from the Antonine Wall, and the pictures which have been added to the original collection. Mr H. C. Gilson thanked the University on behalf of the Society and a pleasant and instructive evening ended with refreshments.

Friday, 5 August

The visit to the Marine Biological Station at Millport, Isle of Cumbrae, was marred by bad weather. The party drove by bus to Largs and then went by small boat to the island. Rough seas made it impossible to land at the Pier and members scrambled up the rocks in pouring rain. The generous welcome and hospitality extended to the party by Dr Ford and his colleagues soon banished any feeling of discomfort, and a most interesting day was spent, chiefly within the Station. Demonstrations illustrating the work of the Station had been prepared, and the aquarium was also open to inspection. Dr S. M. Marshall showed data on the seasonal vertical migration of plankton. Apart from *Microcalanus*, which remains below about 10 m. almost entirely, all other species studied stay mainly at less than 10 m. beneath the surface until mid-June when they migrate downwards so that in July and August they are mainly below 10 m. An upwards migration starts near the end of August. The causal factors are not yet elucidated, but temperature is likely to be involved. Further work by Dr Marshall deals with the seasonal variation in size in Copepods and with the ecology of small Copepods. Botanists were interested in the charts showing the distribution of algae and sessile animals in the intertidal zone. On the moderately exposed shore examined the algal dominants, from above downwards, were *Pelvetia*, *Porphyra*, *Fucus spiralis*, *Gigartina mamilliosa* and *Himantalia* (near M.L.W.N.T.), and finally Laminarians. Other noteworthy data were of the total numbers of different animal species and of animal individuals per unit quadrat, both attaining maxima in the *Fucus spiralis* zone close to M.L.W.N.T. For a short period in the afternoon it proved possible to venture on to the shore where Dr E. Conway demonstrated the algal zonation and the areas in which recolonization was following the removal, in some cases of limpets, in others of all algae, from isolated or non-isolated rock surfaces. Other demonstrations in the Station showed the hydrography of the Millport area and the equipment used for marine research, and Mr Gilson expressed the sincere feeling of the party when he thanked the Director and his colleagues for their kindness and for all the care taken to provide for their interest and comfort. The return crossing proved less troublesome than some members feared and none seemed the worse for the day's trip.

In the evening the Society entertained at dinner in Queen Margaret Hall the Officers of the Andersonian Naturalists' Society of Glasgow. Mr Gilson welcomed the guests and Prof. K. W. Braid, President of the Andersonian Society, expressed his appreciation of the opportunity thus afforded of celebrating the long association of the two Societies. Mr Gilson made this dinner the occasion for thanking all those who had contributed so much to the success and enjoyment of the Glasgow Meeting, and paid special tribute to the work of Dr E. Conway and Mr Hutchinson, of the Department of Botany, who were chiefly responsible for the excellent programme. The Society signified its hearty agreement with all Mr Gilson said.

Saturday, 6 August

On the last day a somewhat smaller party proceeded by train to Craigandoran and thence by boat to Dunoon where buses took them to the Benmore Forestry School and Estate and the Scottish National Forest Park, Benmore, Argyll. After a most instructive and enjoyable day the Meeting closed with the return to Glasgow in the evening.

REVENUE ACCOUNT FOR THE YEAR ENDING 31 DECEMBER 1948

	Income		Expenditure	
	£	s. d.	£	s. d.
Subscriptions received, including arrears, and less Payments in advance				
Members taking <i>Journal of Ecology</i> only	377	10 6		
Members taking <i>Journal of Animal Ecology</i> only	224	15 6		
Members taking both <i>Journals</i>	227	5 0		
Associates	1	2 6		
	830	13 6		
Less reserves to 1949 for second parts of <i>Journals</i>	320	0 0		
		510		13 6
Interest on Investments	72	0 0		
Interest on Deposit Account	3	11 1		
Interest on P.O. Savings Bank Account	37	6 2		
		112		17 3
<i>Journal of Ecology</i> —Sales less costs		878		18 11
<i>Journal of Animal Ecology</i> —Sales less costs		43		17 8
<i>Journal of Ecology</i> , Index to vols. 1-20, Sales	22	10 0		
" " " " less costs	14	10 4		
		7		19 8
				£1554 7 0
<i>Journal of Ecology</i> :				
Sales: Current volume 36, no. 1	303	13 1		
Back volumes and parts	1336	18 6		
Reprints of papers	77	1 9		
				£1717 13 4
<i>Journal of Animal Ecology</i> :				
Sales: Current volume 17, no. 1	241	19 11		
Back volumes and parts	149	13 6		
Reprints of papers	46	13 7		
				£1717 13 4
<i>Working Expenses</i> :				
Meeting expenses	27	0 1		
Travelling	20	2 7		
Printing and Stationery	16	7 9		
Postages	10	19 7		
Clerical assistance	8	10 0		
Addressograph	8	6 0		
Audit Fee	6	6 0		
Wild Life Conservation Memorandum	1	12 6		
Bank charges	10			
		57		13 9
Grant to Freshwater Biological Association		28		17 4
<i>Biological Flora of British Isles</i> : Costs				
" "				
Balance—Surplus for Year				
				£1554 7 0
<i>Journal of Ecology</i> :				
Cost: Paper, Printing, Plates, Binding	636	5 5		
Publishers' Commission	184	5 9		
Carriage, etc.	23	6 1		
Insurance of Stocks	3	10 0		
Cost of Copies bought in	1	7 2		
	838	14 5		
Balance (see above under Income)	878	18 11		
				£1717 13 4
<i>Journal of Animal Ecology</i> :				
Cost: Paper, Printing, Plates, Binding	305	18 2		
Publishers' Commission	83	6 4		
Fee for checking references	20	0 0		
Carriage, etc.	10	6 10		
Insurance of Stocks	5	0 0		
	384	9 4		
Balance (see above under Income)	43	17 8		
				£438 7 0

BALANCE SHEET AT 31 DECEMBER 1948

<i>Assets</i>		£ s. d.		£ s. d.	
Cash in hand at Westminster Bank	622	19	10
Current Account
Deposit Account	700	0	0
Post Office Savings Bank Account	1322	19 10
Publishing Accounts due from the Cambridge University Press:	1571	14 6
<i>Journal of Ecology</i>	1187	17	7
<i>Journal of Animal Ecology</i>	323	0	3
<i>Biological Flora of the British Isles</i>	23	15	6
<i>Journal of Ecology</i> , Index, vols. 1-20	2	0	10
Investments at Cost:	1536	14 2
£1200 of 3½% War Loan Stock	1230	4	1
£700 of 3% Savings Bonds 1960/70	700	0	0
£200 of 3% Savings Bonds 1965/75	300	0	0
	2230	4 1
				£8661	12 7
				£8661	12 7
				£8661	12 7
<i>Liabilities</i>		£ s. d.		£ s. d.	
Members' Subscriptions, prepaid for 1949/50	19 0 6
Library Fund	1 5 0
Printing Accounts due to the Cambridge University Press:
<i>Journal of Ecology</i>	486	2	5
<i>Journal of Animal Ecology</i>	256	11	2
<i>Biological Flora of the British Isles</i>	45	6	6
Sundry Accounts due	788 0 1
Reserve of Subscriptions for 1948 allocated to second parts of each Journal:	2 10 5
<i>Journal of Ecology</i> , Vol. 36, no. 2	188	10	0
<i>Journal of Animal Ecology</i> , Vol. 17, no. 2	131	10	0
General Revenue Account—Surplus in hand:	320 0 0
Balance at 31 December 1947...	4114	11	10
Surplus for the year 1948	1416	5	3
			...	5530	17 1
				£8661	12 7
				£8661	12 7
				£8661	12 7

A further Asset, not valued, is the Unsold Stock of Journals, Index Volume and *Biological Flora* Reprints held by the Publishers for the Society.

VICTOR S. SUMMERHAYES
ALEX. S. WATT
Hon. Treasurers.

Audited and found correct, and as shown by the Account Books of the Society.
The Bank Balance has been verified by Bank Certificate, and also the Investments.

WM NORMAN & SONS
Chartered Accountants

120 BISHOPSGATE, E.C. 2
and
231a HIGH ROAD, LOUGHTON, ESSEX
4 May 1949

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